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BIOLOGY
OF APHID PARASITES
(Hymenoptera: Aphidiidae)
WITH RESPECT TO
INTEGRATED CONTROL

BY

PETR STARÝ



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"Our modern culture is developing greater and greater control over man's environment—the planet earth. Although we may poke out into space a bit, our immediate future is here on earth. We must come to peaceful terms with ourselves and our environment if we are to survive. Time is running out. Our material resources are being depleted and our numbers at the same time are increasing at an astonishing rate. I am an optimist—I think we can maintain this planet as a fit place to live and I think the integrated pest control approach is an essential part of the future scheme of things. Let's get on with the job."

Ray F. SMITH
Annual Meeting of
Western Forestry Pest Communities,
Western Forestry and Conservation Association,
San Francisco, California,
December 10, 1963

TO MY PARENTS

Introduction

Observations on various groups of entomophagous insects were being made for many years. The peculiar and complicated relations between host and parasite were subjects of interest of the earliest authors in entomology. Nevertheless, only the concept of biological control and its further development undertaken by various specialists have greatly stimulated this research trend. The observations on entomophagous insects were carried out purposely—how to utilize them for man. It was soon found that the more or less occasional observations of the early workers showed certain insects to be valuable agents in limiting the population numbers of their hosts, but at the same time, it was found that new viewpoints must be developed and applied in research. Various trends, which are mostly a character of every new research, from overestimating the value of taxonomy to overestimating the value of practical viewpoints, can be found in the history of research of entomophagous insects. A similar situation can be seen to occur as to the relation of entomophagous insects and chemical treatments. Today, and this state can be classified as generally accepted, there is no doubt of the relative value of all the branches, the complex viewpoint being applied.

The above remarks can also be applied to the aphid parasites. The 19th century can be classified as "generally taxonomic", there being the main aspect of research, the composition and description of the fauna in various countries and territories. We can, however, also in that century find many papers where the ecological aspect was stressed also. At about the beginning of the 20th century, besides the further development of taxonomy, more detailed papers appeared on the biology of the groups as well as some papers dealing with the biological control possibilities and experiments. These attempts and trends exhibited various levels and intensity in different countries.

The period of our contemporary era is characterized by revision and further development in taxonomy and, by a higher percentage of biological papers. A basic stone, if we may use this expression, and simultaneously a stimulating factor that directed interest to the group of aphid parasites as agents in aphid control, were the activities of Californian workers connected with the biological control of *Therioaphis trifolii*, an introduced pest aphid of alfalfa in California. This work showed, on the one hand, the great importance of some parasites as control agents as well as further possibilities for obtaining other parasites for the control of other pest aphids. On the other hand, however, a basic lack of information on the parasites became apparent, starting with their specific identification, not to mention data on distribution, biology, etc., all of these being of basic significance in biological control work. Since that time, the praxis exerted a true pressure on the taxonomy and ecology research trends with respect to aphid parasites. However, on the reverse

side, taxonomists and ecologists have opened many problems and new aspects as to aphid control by parasites.

This state of research has naturally resulted in the appearance of a larger quantity of papers on aphid parasites, dealing with all branches from taxonomy to integrated control. A detailed study of these papers undertaken by the author in connection with his research work lead him to the idea of elaborating the biology of aphid parasites in a comprehensive way with respect to their use in the integrated control of aphids. This idea is far from being original. Many books on general biological control have already been published, many of them being prepared by teams of skilled specialists. Generally, there is no doubt that a similar task is rather difficult to fulfill. All branches of research work must be covered adequately, which of course depends on the author's own experience and on the number and quality of various literary records published. Nevertheless, the records are often of unequal value and a necessary generalization may result, and probably does so, inaccurately or even erroneously. Besides, it is not possible, owing to perpetual development of science, to make certain definite statements or viewpoints in different branches as new and new aspects appear. Moreover, the aphidid wasps are a group of parasites, and it has been correctly stated by RÖDINGER & SWIRSKI (1957) as to their hosts—the aphids: "The student of aphids is requested never to generalize". However, a parasitologist needs a certain generalization with respect to a host-parasite relationship.

A complex elaboration may have a basic advantage: the whole matter is explained in a continuous way so that the reader may well understand the various connections and peculiarities. This book is the result of a long study of the world's fauna, field research in different zones and countries and certain laboratory and field praxis in aphid control by parasites. Naturally, in some parts of the book we followed literary sources mostly due to lack of our practical work in certain branches. Similarly, there are various deductions and research projects included in the book that have to be dealt with in the future. This is quite intentional as we want to inform the reader of the problems of the research too, to enable him to become sufficiently oriented in research as well. We have mostly avoided any discussion about certain unclarified problems, more detailed information being found in references added.

The scheme of the book is original too. It may seem to be somewhat complicated to a reader, and it surely is. Moreover, there are many paragraphs that overlap. We find it necessary to show or stress certain connections. To enable the reader to get more detailed information as to the separate themes, corresponding references are given under the separate theme or chapter. Survey of literature pertaining to this book was concluded approximately in the first half of 1967.

In this introductory part of the book, I should like to express my sincere gratitude to Prof. Dipl. Ing. Dr. E. SCHMITZKEK for enabling this work to appear in the "Series Entomologica".

I should like also to add my most grateful thanks to Dr. W. Junk N. V.—Publishers, for their untiring efforts and work connected with the preparation of the complicated manuscript and its publication.

We are indebted to Mrs. B. KLOUČKOVÁ, a native English woman, for her scrupulous care in editing the English language of the whole manuscript, which was a very difficult task, the aim being to bring the somewhat peculiar English style of the author whose mother tongue is Czech, more into conformity with the laws of the English language.

Our cordial thanks are also expressed to Mrs. N. Brázdilová and Miss M. Vavřichová (Institute of Entomology, Czechoslovak Academy of Sciences) for their valuable technical assistance during the preparation of this manuscript.

Prague, December 1967

PETR STARY

Methods

SEARCHING FOR APHIDS AND PARASITES. General problematics of research must be taken into consideration before any work with aphid parasites is begun, to prevent time losses and possible mistakes. There will be a somewhat different approach to the problem in the case of a complex research of the whole aphid parasite fauna of a given territory than in a case where only a single pest aphid species has to be searched for.

— **BASIC RESEARCH** of the parasite fauna of a given country must follow these trends:

1. The composition of the aphidid fauna of the area or country. General knowledge of the basic features of world fauna and knowledge of the fauna of neighbouring countries or areas is necessary in order to understand the distribution of parasites, their biology, etc. Every country is a part of a given zone, and this fact must undoubtedly be taken into consideration.

In every parasite species the following must be mentioned: A. Distribution: Geographic distribution of a parasite is helpful in the classification of the fauna of the country. B. Habitat: Occurrence of a parasite in a given habitat gives information on its distribution in a given zone. C. Host: All aphid hosts known from the country or area are listed. D. Host specificity records must include the general characteristics of host-specificity range of a given parasite species, showing the host preference by the parasite for separate aphid groups or species. E. Phenology. Field observations give many records on the seasonal occurrence of separate parasite species. Their summarizing may provide at least some general knowledge on parasite occurrence, and may show certain peculiarities—such as diapause, etc.,—in addition. F. Economic significance: In this respect, the parasite is classified at first in relation to aphid groups, whether it attacks economic pests or not, if its main host is a pest or not, etc. Further, its significance in limiting the given pest is mentioned. G. Notes. Field observations give a great number of varied detailed observations which have to be mentioned under separate parasite species.

2. Parasite complexes of the main aphid pests and their effectiveness in various ecosystems.

3. Host specificity of the separate parasite species. Field observations based on numerous samples permit us to classify the host specificity of parasites. The host specificity range is one of the basic features enabling the ascertainment of the relation of the parasite to various members of an ecosystem and also to other ecosystems.

4. Natural limitation of aphids by parasites during the season. Field observations usually give only general records about the effectiveness of separate parasite species, however, such records have to be noted, giving at least general information on the significance of a parasite in a given area. A skilled observer may give much helpful information to biological control workers.

Basic research must be started in quite a rational way to represent a true basis for applied research trends. With respect to our experience, basic research must follow the undermentioned scheme:

1. General characteristics of the landscape and rough division into typical kinds of habitats.

2. General knowledge of the biology of aphid species in a given district or area.

3. In different kinds of habitats, except perhaps extensive areas of monocultures, all the aphid species obtainable are collected. If it is possible, the sampling will cover the whole season.

4. In every habitat, especially in cultivated fields, it is necessary to classify the environment, for example, the adjacent areas. In cultivated crop fields it is recommended to take samples from central parts of the fields and from the edges to cover the ecotone problem, parasite dispersal, relations of the ecosystems, etc.

5. Each sample must be labelled and the records put in a catalogue where all field notes are also mentioned (see below).

— APPLIED RESEARCH is directed towards a given pest species and factors influencing its occurrence in a given country. In an integrated control program, the composition, ecology and effectiveness of the parasites are rather important.

SAMPLING. The aphidid group of parasites includes aphid parasites exclusively. This results in relatively easy sampling methods and techniques, as all the sampling activities are directed to a single group of hosts. However, although being a single group of hosts, aphids are occurring today in rather various environments and it is a matter of several years and hard theoretical and practical knowledge to obtain good sampling experience.

— **SAMPLING OF APHID COLONIES.** The best way of obtaining the parasites is to collect aphid colonies on various plants and rear them, although being naturally seasonally dependent, most of the aphid colonies are attacked by parasites. It is not important whether a colony of aphids includes dead mummified aphids—a clear proof of parasite presence—or not, the higher instar parasite larvae, if present in the colony collected, will reach maturity and mummify aphids during 2–3 days before the aphids die, due to lack of food in the samples taken.

The most suitable method is to collect portions of plants with aphid colonies and put them in small glass or plastic vials of approx. 25×60 mm in dimension. A piece of dense nylon texture tied with rubber is put on the open top of the vial to prevent the escape of emerged parasite adults. Smaller portions only are recommended to be put into the vials.

If large portions are put into vials there is danger of fungi developing and spoiling the whole sample.

In every case, we recommend to look through the samples every 2–3 days after being taken in the field.

Sometimes it is necessary to take large samples. A piece of paper, however, must be put on the bottom and also among the pieces of plant to prevent a high condensation of evaporation inside the container; every container must be wide enough at the top, being covered with nylon texture and tied with rubber in a similar way as mentioned for the vials.

Each sample has a sample-number corresponding to the records noted in a notebook. This number is written with an ordinary pencil on a piece of paper and put into the vial. Simultaneously, a certain number of aphids (mature specimens namely) are put into alcohol, with the corresponding number of sample, for better identification later. If necessary, the plant is taken for the herbarium for later identification as



Fig. 1. Field equipment for collecting and rearing of samples. A - scissors, B - notebook, C - pencils, D - pincettes, E - metallic boxes with vials, F - box with alcohol containing vials, G - plastic bottles.

well. In case of the presence of ants, a certain number of specimens are put into alcohol in another vial (Fig. 1, 2, 3).

If a whole natural enemy complex is to be dealt with, never leave the predatory larvae and adults of various insects in the same sample with the parasitized aphids, as the predators continue to feed on the aphids and also destroy the emerged aphidiid adults, either by feeding on them or by a mechanical way.

- SWEEPING. Many aphidiid specimens may easily be taken by sweeping in various localities. The sweeping method has its application mainly if we want to get records on a parasite presence in a certain plant stratum.

- OTHER METHODS. Parasites attacking aphids living on mosses (peat bogs, etc.) may be obtained by putting mossy material into the Tullgren apparatus. Similarly, some parasites are obtained by sifting ant-nest material collected in winter, transferring it to the laboratory and placing it in a Tullgren apparatus.

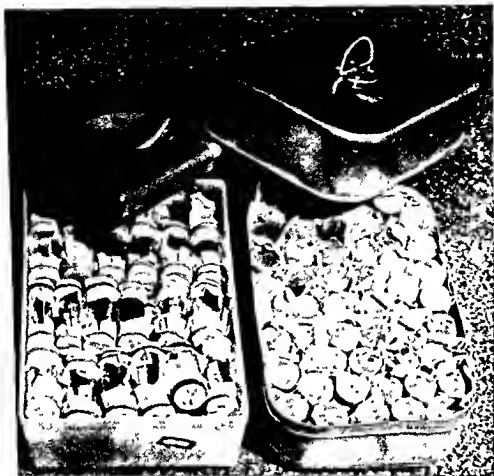


Fig. 2. Field equipment for collecting and rearing of samples. Metallic and plastic boxes with vials.

REARING. Both vials prepared for use and vials with samples are placed in standardized metallic or plastic boxes, about 50 vials in each. The boxes protect the vials against mechanical injury during the trip, and to intensify the protective function we can recommend the placing of a layer of cotton-wool on the bottom of the box. It is recommended to leave the boxes open during a longer stay on a field trip (at night) to enable a better drying-up of plant portions and to prevent the development of fungi. Similarly, they should be deposited in the shade during the day when possible. The plant in the vial is a sufficient food supply for the aphids for 1-2 days, a period long enough for maturing the higher instar parasite larvae. Similarly, the moisture in a vial due to the presence of pieces of plants is sufficient to prevent the drying of parasite cocoons especially at the initial periods of their occurrence.

Samples are left in vials for at least 14 days, to allow the parasites and hyperparasites to emerge. (Fig. 3, 4).

SELECTION. After being reared in the laboratory, the samples in vials contain a mixture of dry plant material, mummified aphids, dry remains of dead aphids, and parasite and hyperparasite adults, or other natural enemies of aphids. Such material



Fig. 3. Above - vials containing samples to rear the parasites. Below - smaller vials containing selected reared material of parasites and aphid mummies.

naturally needs a selection before being of further use. First, the nylon texture and rubber are removed from the top of the vial, the piece of plant is carefully taken out by a pincette and the remains of dead aphids, adult parasites, etc., are dropped out onto a piece of white paper. Further, preliminary selection of material into aphidiid parasites, secondary parasites and other natural enemies follows, every small vial with the material being provided with the corresponding number of the sample. In another vial, associated with the adult aphidiid parasites vial, the remains of plant material with empty aphid mummies are placed, the latter is important for eventual further identification of parasitized aphids in case no living aphids were obtainable or in case that two or more aphid species were present in the sample, to decide which aphid is the true host of the parasite or parasites; further, the coloration of mummified aphids may be useful for parasite identification as well; quiescent and non-quiescent cocoons may be recognized; host instar killed by the parasite larva may be established to derivate the host instar preference by the parasite ♀.

PRESERVING. Both in the field and in the laboratory the best way of preserving the unmounted material is to keep it in small glass or plastic vials, closed by a piece of cotton-wool. In case of laboratory selection the adult parasites may be left freely on the bottom as we can avoid mechanical injury in the laboratory. Another situation



Fig. 4. Bottles for rearing of samples in the laboratory.

exists in the field, where the adult parasites must be carefully put between two pieces of cotton-wool to prevent the movements of material during transport and the whole box must be supplied with a layer of cotton-wool to prevent the material from as many injuries as possible.

MOUNTING. The best method is to glue the parasite adult to a white standardized label 7 x 15 mm by the right side of the thorax, the wings of the specimen are made upwards, the abdomen bent down, as the identification characters on propodeum and first abdominal tergite must be recognizable. The specimen is placed in the upper fourth of the label, in such a manner so as not to leave the antennae and wings reaching over the margins of the label, on the lower margin the sign of sex and the

number of antennal segments are written. Ten specimens of each sample are said to be sufficient for an identification and collection supply, while a larger quantity is mounted additionally in cases of necessity (variability, etc.). The vial with plant remainders and aphid mummies is left with the series of specimens.

Examination of ♀ external genitalia is necessary in the majority of cases. It is necessary to make microscopic slides, the following method being recommended: (1) In a dried specimen, the apical part of the abdomen is carefully removed; (2) The specimen is given the same number as the slide; (3) The removed part of the abdomen is boiled in 10% KOH solution for several minutes, as the thickness of the object requires; (4) The object is washed in distilled water; (5) Then it is mounted as a slide, using DeSwann or DeFaure mounting medium; (6) The records identical with those of the mounted specimens are put on labels placed on the microscopic slide.

IDENTIFICATION. Aphidiids are relatively small insects and the characters on the adult body must be examined when identifying the species. For this reason, a good binocular microscope is necessary. In addition, characters on the female genitalia and often on other parts of the body must be examined when mounted as slides, a microscope of approximately 1500x magnification (maximally) being at hand as well.

The aphidiid wasps are a group of parasitic Hymenoptera for which a certain training and routine in examination is necessary. We can recommend for a worker, who starts the work in the research of aphidiid wasps and is not experienced in the taxonomy of other groups, to begin with the identification of the material to a generic level, identification to species level being dealt with after somewhat more comprehensive material of separate genera is at hand to understand the classification mentioned in the keys. In every case it is recommended to begin the identification with a series of reared material, while swept material is much more difficult. Basing the initial identification on the comparison with material which was identified by a specialist can be of some help.

-SYNOPSIS OF DIAGNOSTIC CHARACTERS. Only a general brief review of diagnostic characters is mentioned below to suggest general information to the reader.

Head.—Shape transverse or square, strongly or arcuately narrowed behind eyes. Dimensions on the head: width of head in comparison with thorax, interocular line, facial line, transfacial line, clypeoantennal line, tentorio-ocular line, intertentorial line, socket-ocular line. Eyes are of various size and prominence, oval to nearly hemispherical, convergent to the clypeus. Clypeus is transverse, bearing long and more or less dense hairs. Antennae are filiform, rarely moniliform, number of segments is variable, being mostly different in ♂♂ and ♀♀; usually the relation of F_1 to F_2 as to length is important; presence or absence of rhinaria on the segments is sometimes a useful character being generally variable; apical and prapical segments may be fused.

Thorax.—The declivity of mesoscutum to prothorax is sometimes a good character. The pubescence of the lobes of the mesoscutum is different—either there are rows of hairs along the mostly effaced notaulices and margins, or hairless spots on the discs of lateral lobes. The notaulices are of various length and depth, sometimes entirely effaced, usually being visible in the ascendent part of mesoscutum, rugose or crenulate and wide and effaced on the disc, rarely reaching the praescutellar groove.

Wings.—Shape, length and width of pterostigma. Length of metacarpus. Length of various veins, relations between veins, etc.

Legs.—Legs are usually homogeneous, slender and long, rarely strong and short.

Abdomen.—It may be lanceolate or rounded. Tergite 1 may be square, or longer

12,5 cm

	Sample No.
Locality	
Habitat	
Aphid Host Plant	
Aphid	
Notes	

7 cm

	1965/680
San Fernando, env. of Guantánamo, Oriente prov., CUBA, 21 6 1965 (Starf)	
Field - edge	
Eupatorium sp.	
Aphis apiceae Patch	
High percentage of mummified aphids	
A weed plant.	

Parasite	Country
	Sample No.
Host Aphid	
Aphid Host Plant	
Habitat	
Notes	
Locality	

Lysiphilus testaceipes (Cress.)	CUBA
Aphis apiceae Patch	1965/680
Eupatorium sp.	
Field - edge	
High percentage of mummified aphids.	
A weed plant.	
San Fernando, env. of Guantánamo, Oriente prov., CUBA, 21 6 1965 (Starf)	

Host Aphid	Country
Parasite	Sample No.
Aphid Host Plant	
Habitat	
Notes	
Locality	

Aphis apiceae Patch	CUBA
Lysiphilus testaceipes (Cress.)	1965/680
Eupatorium sp.	
Field - edge	
High percentage of mummified aphids.	
A weed plant.	
San Fernando, env. of Guantánamo, Oriente prov., CUBA, 21 6 1965 (Starf)	

Fig. 5. Sample, parasite-host and host-parasite, filing cards for catalogizing records.

than wide, its sculpture is various: smooth, rugose, rugose-punctuate, bearing carinae, etc.; spiracular tubercles may or may not be predominant, sometimes secondary tubercles may be recognized (not bearing spiracles) in the portion between spiracular tubercles and apex; the relative dimensions between width, length, and tubercles are important characters. External genitalia of ♀: Shape, pubescence of ovipositor sheath, to a lesser degree also the shape of prongs of second valvulae, etc.; ovipositor sheath is of various shape: triangular and trifid at extremity, or prolongately arcuate and obtuse at the apex, or curved downwards and narrow or plough-share shaped; or curved downwards and widened at apex, etc.

Coloration represents sometimes valuable character, sometimes it is variable with respect to area and season. Mostly, females are lighter than males.

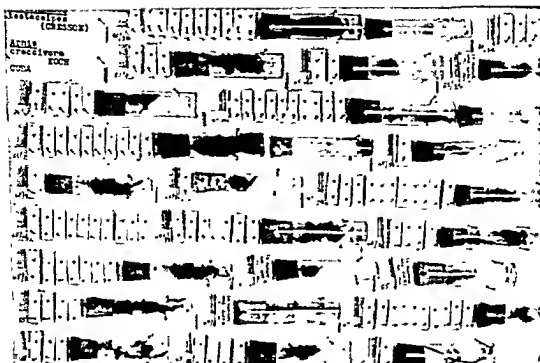


Fig. 6. Collection of aphid parasites.

RECORDS AND COLLECTION. Principally, there are two main parts of the work, i.e. (A) catalogue of samples, and (B) collection, which are organized in a close mutual dependence.

— **CATALOGUES.** Three kinds of catalogues at least are necessary, to have the records ready at hand. Filing cards of 12.5×7 cm are used (Fig. 5).

— **Catalogue of samples.** In the field, all the records of samples are put under given numbers in a note-book, corresponding numbers being also given to the plants, rearings and aphid material in alcohol. In the laboratory, after returning from the field, all these records are transferred to the filing cards and organized in accordance with their numbers in the catalogue of samples. In this catalogue, too, the results of aphid and plant identification are later filled in as well.

— **Parasite—host and Host—parasite catalogues.** Both these catalogues are filled simultaneously, being dependent on each other. After all the identification records, i.e. plant, aphid and parasite are known, the filing cards are typed in a corresponding manner (Fig. 5). Moreover, when dealing also with hyperparasites, we can complete the records in a similar way with respect to separate groups of hyperparasites.

— **COLLECTION.** The material in collection has to be divided into several groups:

— **Mounted unlabelled material.** The selected material of reared primary parasites is mounted and corresponding numbers of samples are put under the first specimen.

— **Mounted labelled material.** Gradually, the mounted specimens are labelled, the labels including all the data (except perhaps the notes) which are on sample-cards, i.e. locality, habitat, aphid host plant, aphid, and sample-number.

— **The collection.** Because of easy orientation, the collection has to be organized alphabetically. In each genus, the separate species are organized with respect to the host, thus enabling a further study of separate biological races, etc.

As usually we find a certain number of species which we are unable to identify for the time being, it is useful to put them in separate boxes under different genera, under the label "spp."

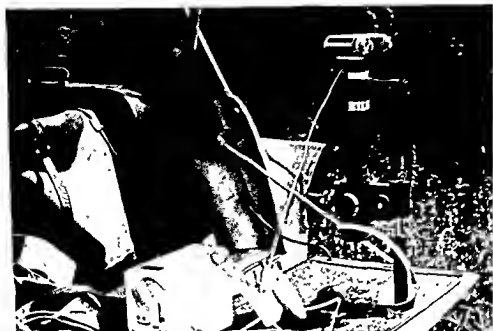


Fig. 7. Photographing in the field. SM-XX binocular microscope with MF-equipment.

As to the boxes in which the material is preserved, we have found most useful the boxes commonly used in Europe, of the dimension 23×30.5 cm, made partly from wood and carton paper, dry peat (1 cm) layer mounted under white paper being used as a substrate in which the pins are stuck. The boxes are comparatively small, well and easily transportable and organizable (Fig. 6).

PHOTOGRAPHING. Photographs of separate habitats, various aphid colonies, aphid mummies, etc. are rather useful for ecological studies. They also may be rather helpful as information suggested by a local worker to a foreign specialist who needs more detailed information. (Fig. 7).

REFERENCES. 696, 997, 1019, 1069, 1117, 1125

Morphology and Anatomy

EGG. The egg of the aphidiids (Figs. 72, 73, 92, 95) is of microscopical dimensions. For example, the egg of *Ephedrus plagiator* is 0.080 – 0.100 mm in length and 0.016 – 0.024 mm in width, that of *Lysiphlebus saharum* 0.086 mm and 0.036 mm, respectively (IVANOVA-KAZAS, 1961). The superficial membrane of an egg forms the chorion, which does not show any structure. The shape and size of aphidiid eggs is specific. The ovarian eggs may be lemon-shaped, spindle-shaped, prolonged, etc.

LARVA. The first instar larva (see: figures of larvae, Figs. 77-93, 98, 194, 213, 219, etc.) is rather typical in all the genera and species. A distinct head with large and prominent mandibles can be recognized, besides the 13 body segments. The mandibles are unidentate. The body segments are often covered with rows of spines or bristles. The last body segment bears a caudal appendage or even additional prongs. In most aphidiids, the caudal appendage is simple and covered with small spines or bristles. In the genera *Ephedrus* and *Praon* there are two perpendicular additional prongs besides the caudal appendage. In the genus *Lipolexis* the caudal appendage is rather long and there are two shorter oblique additional prongs.

The second instar larva is mandibulate, with the mandibles similar to the first instar larva. The segmentation of head and body is less apparent. There are only rare spines or bristles on the body segments, the caudal appendage is distinctly shorter and the additional prongs are missing.

The third instar larva is emandibulate. There are no spines or bristles on its body, the caudal appendage is practically lacking.

The fourth instar larva is mandibulate. The mouthparts are well differentiated (Fig. 84). The antennae may also be well distinguished. The cuticle is covered with minute tubercles. The spiracles are well distinguishable, being in function, the tracheal system is also distinct. Through the larval skin, we can easily differentiate the internal organs. The silk glands can be well distinguished as well as their opening below the oral cavity. The alimentary tract is complete and terminates by the anus. Cerebral ganglia and also the nerve cord are well visible. Numerous whitish corpuscles, the fat bodies, are rather typical. The morphological features of the last instar larva exhibit generic differences (shape and structure of spiracles, etc.).

There are several opinions on the number of larval instars and consequently on their morphology and anatomy in the aphidiids. We have followed TREMBLAY (1964) who gives also a brief discussion on the whole problem. Possibly the number of larval instars varies in dependence on food, etc.

PREPUPA. The prepupa closely resembles the last instar larva but it is shorter, the differentiation between the segments and lateral folds is more distinct and further

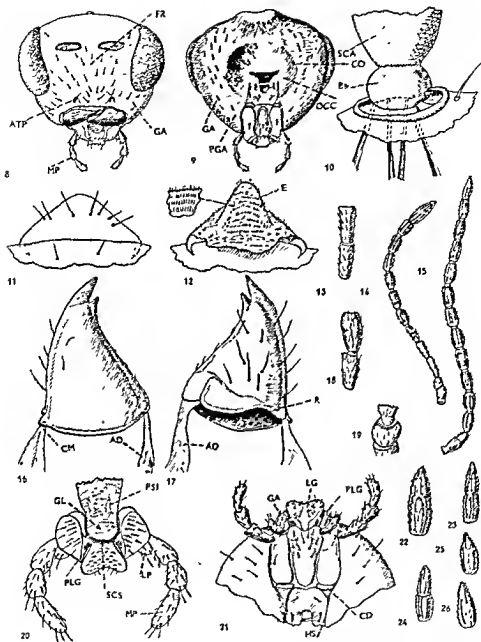


Fig. 8-26. 8. *Lysiphicbus fabarum*, head, frontal view. 9. Head, from behind. 10. Attachment of the antenna. 11, 12. Labrum and allied portions. 13. Flagellar segment 1 and 2. 14. Antenna. 15. Antenna, ♂. 16. Mandible, ventral view. 17. Mandible, dorsal view. 18. Flagellar segment 1 and 2, ♂. 19. Pedicel. 20. Maxillo-labial complex, frontal view. 21. Maxillo-labial complex, ventral view. 22. Last flagellar segment. 23, 24. Apex of antenna, ♀. 25, 26. Last flagellar segment, ♂. (all figures redrawn from TREMBLAY 1966).

Abbreviations (figs. 8-76): AA - aual aperture, AAM - anterior marginal apophyses of urite IX, AC - apodema cervicalis, ACO - copulation aperture, AD - apodeme of adductor muscle, AF - apodema furcalis, ANP - processus alaris anterioris of mesonotum, ANT - antenna, AP - apodema metapleuralis, APF - apodema pleurofurcalis, AR - arolium, AS - arcus, ATP - anterior tentorial pit, AX - axilla, BA - basalar, Bb - basal bulb, Bs - basisternum, C - articulation of valvifer 1, CCX - coxal condyle, CD - cardo, CM - condylus mandibularis, CO - carina occipitalis, CS - cervical sclerite, CX - coxa, D - articulation of first valvifer, DU - ductus of poison gland, E - epipharynx, F - fovea pleuralis, FE - femur, FR - frons, FS - transscutal fissure, FU - furcula, G - sclerite-ligamentum, GA - galea, GAC - acid gland, GC - alkaline gland, GE - gena, GL - glossa, GS - lamina parameralis, GSP - glandula spermatica, HS - hypostomal suture, I - intestine, IGG - epistomal sulcus (clypeoantennal inflections), IT - transverse maxillary thickening, LE - ligamentum, LG - ligula, LP - labial palp, MP - maxillary palp, MPF - mesophragma, MSF - mesofurca, MSC - mesoscutum, MSCL - mesoscutellum, MSEP - mesepimeron, MSEP - mesepisternum, MSF - mesofurca, MST - mesosternum, MT - metanotum, MTF - metafurca, MTP - metapleura, O - ovum (egg), OB - orbicula or manubrium, OBP - oblong plate, OCC - occiput, OD - oviductus communis, P - pleurostoma, PA - processus alaris mesopleuralis, PE - proepisternum, PEM - proepimeron, PEN - penis, PF - praefragma, PGA - postgena, PLG - paraligula, PM - humerale, PMX - palpus maxillaris, PN - mesopostnotum, PNP - processus alaris posterioris, PP - propodeum, PS - parascutellum, PSC - processus scutellaris, PSI - internal sclerites of glossa, PT_{1,2,3} - pteralia, PTEN - pons tentorialis, QD - quadrate plate, R - cavity for the cranial articulation of the mandible, R_{1,2} - rami of valvulae 1 and 2, S_{1,2,3} - sternite, SA - subalar, SB - venom reservoir, SC - cervical sclerite, SCA - scapus, SCS - aperture of silk gland, SE - sensilli, SM - outer sheath, SN - sulcus notalis, SP - spiracle, SPR - spur, SPC - spermatheca, SPS - notaulices (sutura praescutalis), SSS - scuto-scutellar suture, ST - sutura transscutalis, STS - stipes, T1-10 - tergite 1-10, TA - tarsus, TES - testes, TG - tegula, TI - tibia, TR - trochanter, UN - unguis, UT - unguitractor, V_{1,2,3} - valvula 1, 2, 3, VF_{1,2} - valvifer, VS - vesicula seminalis.

bends become recognizable on the body. Extensive changes in internal organs due to the process of histolysis of the larval organs and development of adult organs occur during this state.

PUPA. The pupa (Figs. 87, 88) is of exarate type. The legs and wings are folded to the body. The folded wings are very small and inconspicuous in the young pupa, while in an older one they cover most of the lateral sides of thorax, abdomen and legs. The young pupa is at first yellowish to yellowish white and the coloration becomes gradually darker as the pupa grows older; the compound eyes become pigmented first. The antennae are laid along the ventral side of the body. The internal organs of the pupa are practically identical with those of the adult.

ADULT. The aphidids are relatively a rather uniform group of parasitic Hymenoptera and this feature seems to be due to their full adaptation to parasitism on a single group of hosts, the aphids.

The head (Figs 8-29, 31) is orthognathous, transverse to subquadrate, bearing eyes, three ocelli and the appendices. The face, which forms about the frontal part of the head, is mostly smooth, with more or less dense hairs. Its lower part is formed by the clypeus which covers the greatest part of the labrum. The clypeus is more or less convex, usually oval, mostly smooth, bearing several shorter or longer hairs, it is separated from the face by an arcuate furrow. On the sides of the clypeus are the tentorial pits, which indicate the joining of a part of the head endoskeleton. The top of

the head forms the vertex, separated from the occiput by the occipital carina; it is declivous to the foramen occipitale. The portion of the head behind the eyes and beneath them is called the gena, whose upper portion between the hind margin and occipital carina is called the temple. The width of the gena depends on the size of the eyes and tentorial pits.

The appendices of the head form the mouthparts and the antennae. The mouthparts consist of the labrum, the mandibles, and the labio-maxillary complex. The mandibles are bidentate, more or less prominent, with sparse hairs on the external portion. The maxillae and the labium are united by membranes and form the labio-maxillary complex. Each maxilla consists of the cardo, which is connected with a process of the hypostoma. To its distal portion the stipe is joined, which bears the palpus maxillaris on its apex. The maxillary palp is mostly 4-segmented, sometimes it consists of 3 or 1 segment or it is absent; the number of segments is different in various genera (see: EASTOP 1966). On its external side, the cardo bears two lobes, the galea and the lacinia. The labium consists of the submentum, the mentum and the prementum. On the external distal apex of the prementum the labial palp is joined. The labial palpi are always shorter, mostly 3-segmented, sometimes 1 or 2-segmented or they are lacking completely (see: EASTOP). The chaetotaxy of the mouthparts seems to be characteristic for most of the aphidid genera.

The antennae are mostly filiform, less frequently submoniliform to moniliform, with a varying number of segments (10–30). The basal bulb of the antenna is fixed inside the antennal socket by a membrane and muscles. The first antennal segment is called the scape, the second the pedicel and the rest of the antenna is called the flagellum. The antennae are more or less pubescent, bearing various numbers of the rhinaria. Most of the segments of the flagellum are equal, less frequently the middle segments differ in size and shape; the apical segment is always different, sometimes it is fused with the praepical segment. The number of antennal segments is mostly different in ♂♂ and ♀♀, being higher in the ♂♂; only in the genus *Ephedrus* both sexes have the same number of segments.

The endoskeleton of the head forms the tentorium, which represents a recourse for muscles, alimentary canal, etc.; it is composed of the rami.

The head is connected with the thorax by the cervix, formed by the cervical membrane, which joins the cervical sclerites that are connected with the proepisternum.

The second part of the body, the thorax, consists of the three main parts, the prothorax, the mesothorax and the metathorax. The propodeum is joined to the thorax, which is originally the first segment of the abdomen (Figs. 30, 32–35). The thorax bears the appendices, the legs and the wings.

The prothorax consists of the pronotum, which is connected with the mesonotum at the upper side; the propleurae are relatively weakly joined at its lower sides. The prothorax is mostly smooth, the propleurae bear several hairs and they may be slightly sculptured, especially along the carinae. The endoskeleton of the prothorax is formed by the cristae and the apodemes. The prothorax bears a pair of fore legs.

The dorsal part of the mesothorax is the mesonotum, which is subdivided into two main sclerites: the mesoscutum and the (meso)scutellum. The mesoscutum can be declivous to the head or it can be strongly raised above the prothorax to almost gibbous. It is usually smooth, with slight rugosities near its margins. The pubescence of the mesoscutum is variable, either completely densely pubescent or only several hairs are present. The mesoscutum often bears two furrows, the notaulices. These furrows are distinct at the base only, or they may be distinct as far as the praescutellar groove and thus dividing the mesoscutum into three lobes, or they may be missing completely. The sculpture of the notaulices is variable, they usually are more or

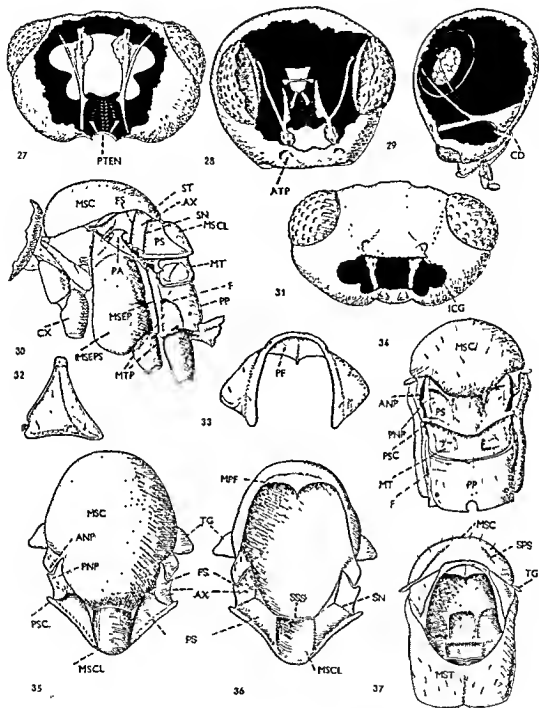


Fig. 27-37. 27, 28, 29. *Lysiphlebus fabarum*, head, endoskelet. 30. Thorax, lateral view, 31. Head from below, partial section to show the endoskeletal parts. 32. Pronotum, lateral view. 33. Pronotum, ventral view. 34. Thorax, dorsal view. 35. Mesonotum, dorsal view. 36. Mesonotum, ventral view. 37. Thorax, ventral view, interior portions. (all figures redrawn from TREMBLAY, 1966).

less crenulate, rugose or almost smooth. The mesoscutum is separated from the following sclerite, the (meso)scutellum, by the praescutellar groove that is of various depths and widths. The scutellum is generally triangular, smooth, more or less convex; its margins are often crenulate. On the sides of the scutellum, there are nearly smooth lateral discs of the parascutellum and of the axillae. The mesopleurae have their lateral sutures usually crenulate, they are rarely slightly sculptured in the upper portion below the wing or they are weakly granulated. The endoskeleton of the mesothorax forms the mesopostphragma, the apodemes, cristae and the mesofurca. The mesothorax bears a pair of fore wings and a pair of middle legs.

In the apical part of the metathorax there is a more or less visible tubercle, the postscutellum, on whose sides there are flat and usually smooth to slightly sculptured impressions. The metapleura and the mesopleura are closely connected with the propodeum. The endoskeleton of the metathorax consists of the apodemes, the cristae and the metafurca. The metathorax bears a pair of hind wings and a pair of hind legs.

The last part of the thorax is the propodeum. It is convex and declivous to the joint-point of the abdomen. It can be almost smooth or it may have various sculpture, being covered with sparse hairs to densely pubescent; various carinae divide the propodeum into the areolae of various sizes and shapes.

The wings (Fig. 107). There are two pairs of wings developed in the aphidids; there is one exception only in the whole family, *Diaeretellus ephippium*, whose ♀ is wingless. The venation of wings exhibits several types of reductions when compared with the most complete type (*Ephedrus*) which is described below. In the fore wing, the fore margin represents the strongly sclerotized fused costal and subcostal vein (and probably the radial vein too), which dilates at the apex and this dilation is called prostigma. The pterostigma is triangular; its prolongation, the metacarp, reaches the wing apex. From the lower side of the pterostigma the radial vein extends, composed of three abscissae and reaches the wing apex where it joins the metacarp and thus completes the pterostigmal cell. Under the fused costal and subcostal vein there is the basal cell, bordered on the external side by the basal vein and on the lower side by the cubital vein, reaching the wing apex. Between the radial and cubital veins lies the median vein, originating in the basal vein and pointing to the wing apex. It consists of three abscissae. On the upper side of this vein there are the radial cells, separated from each other by two interrational veins. On the lower side, there is the median cell, separated on the external side by the intermediate vein. Under the cubital vein there are two cubital cells, separated from each other by a transverse vein, the nervulus, and by the anal vein on the lower side. Hind wing: on the upper margin there is a short fused costal and subcostal vein that deviates after a certain distance from the wing margin and prolongates as the subcostal vein. The radial vein is almost undeveloped and it is as distinct as a small point only on the lower side. Under the costal vein and the subcostal vein there is the cubital vein which restricts the basal cell with the above mentioned veins, which is closed on the external side by the basal vein. Under the cubital vein is the remainder of the anal vein visible at the fore part. There are many types of reduction of venation and they may be recognized from the key to the genera and subgenera (see: chapter V.). The wings are mostly hyaline, rarely they are smoky or bear dark spots. The surface of the wings is covered by short and dense hairs, the lower margin of wings may be covered with short or long hairs.

The wings (Figs. 50, 52, 54, 55) articulate with the thorax by two processes of the notum of the given segment (mesothorax and metathorax), with the fore and hind notal processes. In the lower part, the wing articulates with the pleural process. The

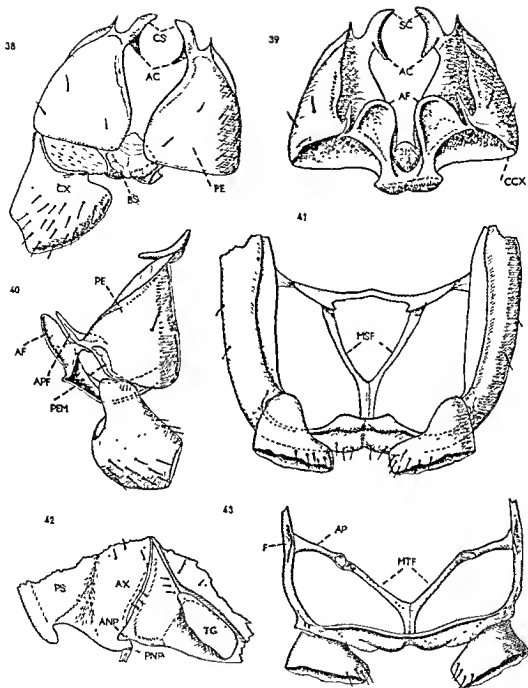


Fig. 38-43. 38. *Lysiphlebus fabarum*, sterno-pleural region, ventral view. 39. Endoskeleton of prothorax. 40. Sterno-pleural region. 41. Endoskeleton of mesothorax. 42. Mesonotum, lateral view. 43. Endoskeleton of metathorax. (all figures redrawn from TREMBLAY, 1966).

lower part of the wing membrane has the appearance of a ligament and is called the axillary cord. Around the wing base the following sclerites are situated, the pteralia: tegula, humeral plate, four axillary plates (acropteral, propteral, mesopteral, meta-ptereral). The acropteral plate articulates with the base of the costal and subcostal veins, the propteral plate with the base of the cubital vein and by the intermediary sclerite also with the base of the anal vein. The lower part of the anal vein articulates with the mesopteral plate.

Winglessness is rather rare among the aphidids. Only a single case of wing modification is known and it is a case of a secondary modification, that is obtained during life. It is known in *Paralipsis enervis*: as the ♀♀ of the parasite attack underground aphid sattended by ants and just the ants nibble parts of the parasites, wings and keep them as symphills.

The legs (Figs. 45-49, 51, 53) are mostly slender and relatively long. A leg consists of the coxa, the bisegmented trochanter, the femur, the tibia, the tarsus and the praetarsus. The tibia bears two spurs at its apex. The praetarsus bears two simple claws, between which there is a small arolium. The first pair of legs bears a cleaning apparatus of tibio-tarsal type.

The abdomen (Figs. 56-76, 99-105) is either rounded or lanceolate. The shape of the abdomen may be also of a sexual dimorphic character and then it is lanceolate in ♀♀ and rounded in ♂♂. The first abdominal segment which may be seen in the abdomen is in reality the second segment, as the first abdominal segment is the propodeum. Nevertheless, for simplicity, we keep the first segment recognizable in the abdomen for the first abdominal segment. Namely the first tergite is of a rather different shape and size in separate genera and species: it is longer than wide or square, more or less convex, almost smooth to coarsely rugose, with sparse hairs to densely pubescent. The spiracles are on its sides, placed on more or less prominent spiracular tubercles. These spiracular tubercles are in some genera called the primary tubercles as secondary tubercles not bearing spiracles can be developed in addition. In separate segments of the abdomen, the tergite and the sternite, connected by a membrane, may be distinguished. Both tergites and sternites are comparatively weakly sclerotized. Six pairs of spiracles may be found in the abdomen. All the abdominal segments are freely connected with each other except segments 2 and 3 which are fused, but the fusion is flexible. The genital segments of the abdomen bear the external genitalia.

External genitalia of the female. The ovipositor consists of the appendices of the primary eighth and ninth abdominal segments. Its apex may be simple, or somewhat dilated, or bear several smaller teeth. The base of the ovipositor is formed by the first and second pair of the valvulae, which are gonapophyses of bases of primary extremities of segments 8 and 9. The ramus of valvula 1 connects with valvifer 1 which is the base of urit 8. The ramus of valvula 2 is attached to valvifer 2, which is probably the coxite of the primary urit 9. The first valvifer, although it belongs to urit 8, is connected with abdominal tergum 9; the second valvifer articulates with the first one. With the distal end of every other valvifer the valvula is connected (*gonostylus*). A pair of valvulae 3 represents the sheaths of valvulae 1 and 2. The valvulae 3 are commonly called ovipositor sheaths. They are sparsely or densely pubescent, but always bear several sensory hairs at their apex. The size and shape of the ovipositor sheaths is rather different in separate genera and species, they can be almost straight to upwards or downwards curved, pointed or obtuse at the apex, narrowed, ploughshare-shaped, etc.

External genitalia of the male. They are formed by the gonopods of the primary segment 9 and by the penis. The greatest sclerites of these organs are the gonocoxites. On their lateral-apical margin the gonobase is attached, which is probably formed by the fused basal parts of the primary gonocoxopods. On the internal ventral side of each gonocoxite a sclerite, the volsella, is attached. The external prong of this volsella is called the cuspis, and the internal one is the digitus. To the distal end of each gonocoxite the gonostylus is attached. All these parts form the gonoforceps. The penis is protected by the sheaths, the penis valvae, which are primarily the basal processes of gonocoxopods which have separated themselves during evolution.

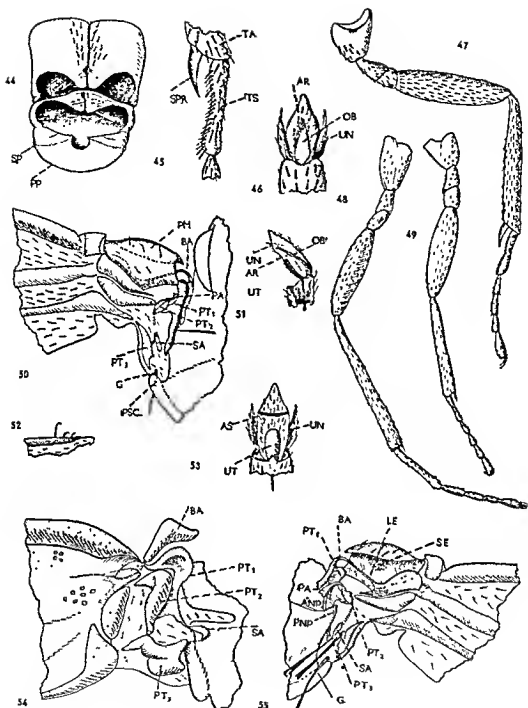


Fig. 44-55. 44. *Lysiphlebus fabarum*, meso- and metasternum, ventral view. 45. Part of fore leg to show tibio-tarsal cleaning mechanism. 46. Arolium, dorsal view. 47. Fore leg. 48. Hind leg. 49. Middle leg. 50. Articulation of fore wing, dorsal view. 51. Arolium, lateral view. 52. Hind wing, detail of setae. 53. Arolium, ventral view. 54. Articulation of hind wings. 55. Articulation of fore wing, ventral view. (all figures redrawn from TREMBLAY, 1966).

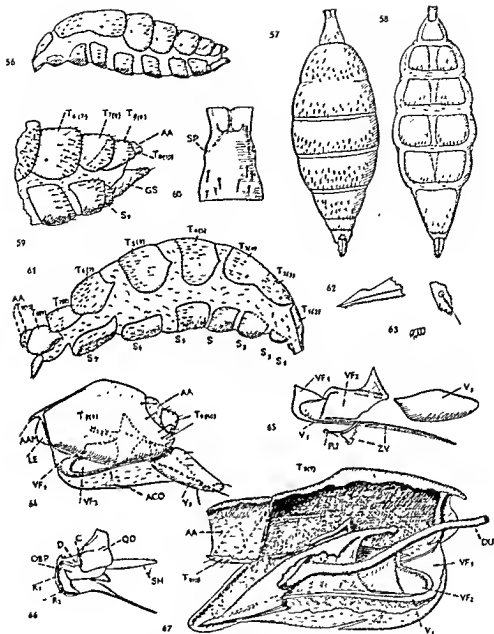


Fig. 56-67. 56. *Lysiphebus fabarum*, abdomen, ♂. 57. Abdomen of ♀, dorsal view. 58. Ditto, ventral view. 59. Abdomen of ♂, apical portion. 60. Tergite 1. 61. Abdomen of ♀, lateral view. 62. Apex of ovipositor. 63. Sensilles at apex of ovipositor sheaths. 64. ♀ genitalia. 65. ♀ genitalia. 66. ♀ genitalia (after SODGRASS). 67. ♀ genitalia, interior view. (all figures redrawn from TREMBLAY, 1966).

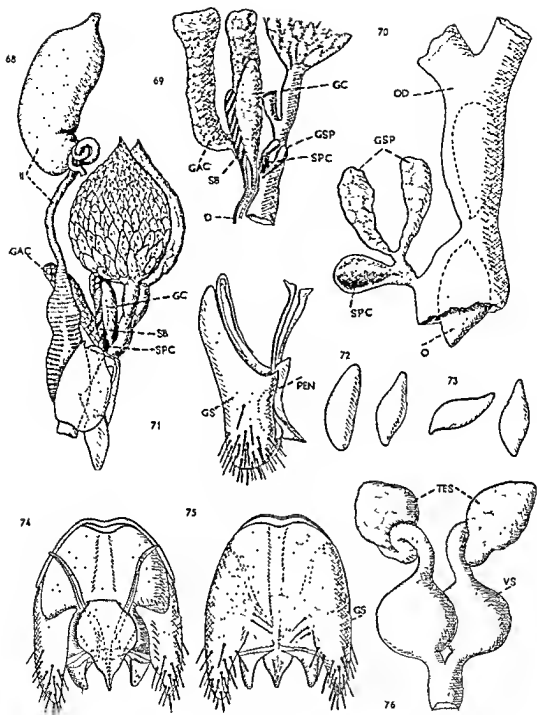
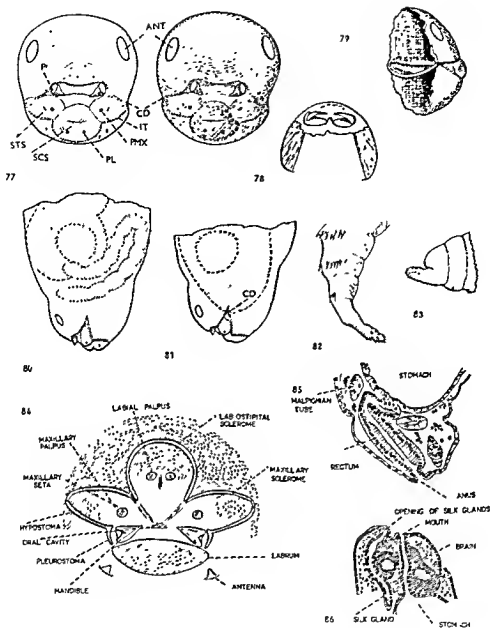


Fig. 68-76. 68. *Lysiphlebus fabarum*, ♀ genitalia, internal parts. 69. Ditto, detailed. 70. Ditto, detailed. 71. ♂ genitalia, lateral view. 72. Egg. 73. Ovarian egg. 74. ♂ genitalia, dorsal view. 75. Ditto, ventral view. 76. Ditto, internal portions. (all figures redrawn from TREMBLAY, 1966).



Modifications of the abdomen. A special modification of the abdomen may be found in the ♀ of *Protaphidius wismanianii*, whose tergites 1, 2 and 3 are normal, only tergite 3 is strongly narrowed to the apex. Beginning with tergite 4 the following tergites of the abdomen are tubiform and thus form a kind of sham-ovipositor. The external genitalia are situated as usual.

In some highly specialized genera various accessory apparatus, enabling a better attack of the aphid, are developed. In general, two kinds of apparatus of this kind can be recognized: in *Trioxys* two prongs are developed in the last abdominal sternite. In *Acanthocaudus* a similar system is developed, but the ventral prongs bear several smaller prongs at their basal portion. In *Bioxys* there is only a single ventral prong. In *Metaphidius* the apparatus is of a different kind. It is formed by the tubiform prong at the base of tergite 6.

Coloration. Black, brown, orange and yellow and their combinations are the commonest colours in the adults. Within the frame of a species, the coloration varies, first in dependence on the part of distribution area, where the more obscure forms are found in northern areas and the lighter coloured forms in the southern areas. Secondly, the coloration varies also depending on the season in a given place, the more obscure colours prevailing in spring and autumn (colder periods of the year), while lighter colours are typical of the hot summer period. Further, the coloration is influenced by the host size which determines the size of the parasite.

Size. The size of the adult body within the frame of a species is widely dependent on the size of the host, which is rather variable in widely specialized species.

Internal anatomy. With the exception of perhaps the reproductive organs, the internal anatomy of the aphidids does not seem to differ significantly from the other parasitic Hymenoptera. As to the alimentary system, the external mouthparts have their role in distinguishing, accepting and transporting food to the internal parts of the tract. The oesophagus is long and narrow, it runs from the mouth through the head and down to the abdomen, where it is enlarged and forms a large and thin-walled crop (ingluvies). The latter is followed by a small gizzard, which is thick-walled. The gizzard passes into the mesenteron, which is large, with secretory cells in its walls. The Malpighian tubes lead into the mesenteron at the junction of the mesenteron with the proctodeum. The rectal portion of the alimentary tract is slightly enlarged and this part, which is called the rectal glands, is more glandular than the other parts of the rectum. The rectum is terminated by the anus, which opens at the dorsal posterior end of the body, above the opening of the reproductive system. The circulatory system exhibits the general features known to occur in the other Hymenoptera and the same can be said about the respiratory system. As to the nervous system, there are the cerebral ganglia and the suboesophageal ganglia in the head, which are united by the circumoesophageal connectives. This mass, which is commonly called the brain, is continuous with the ventral nerve cord. This cord is formed by the three thoracic ganglia, of which the second and third are almost fused, and further by the five abdominal ganglia, of which the last one is the largest. As to the locomotory system, the most powerful musculature is in the thorax.

Reproductive system (Figs. 68-73, 76, 99-105). The first part of the female reproductive system are the ovaries. As far as is known, it seems that there are two different groups recognizable: in the first group, represented by the genera *Ephedrus* and *Praon*, the ovaries are divided into 2 long ovarioles which reach, being folded, as far the base of the abdomen. The second group, which includes the genera *Aphidius*, *Diaeretiella*, *Lysiphlebus* and *Trioxys*, the ovaries are more or less drop-formed. Fully developed eggs occur in the posterior region of the ovaries while eggs in various developmental stages, surrounded by a follicle of nutritive cells, may be

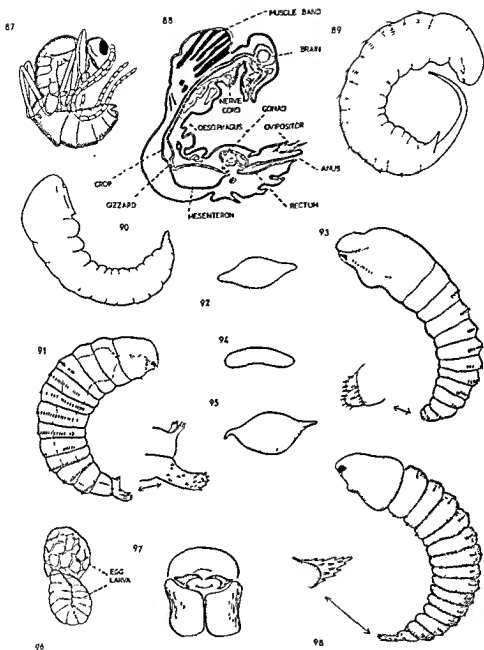


Fig. 87-98. 87. *Aphidius avenae*, pupa (MACGILL, 1923). 88. Ditto, a section through pupa (MACGILL, 1923). 89. *Lipolexis gracilis*, instar I larva. 90. *Monoctonus angustivalvus*, instar I larva. 91. *Praon exoletum*, instar I larva (SCHLINGER & HALL, 1960). 92. *Trioxys complanatus*, ovarian egg (SCHLINGER & HALL, 1961). 93. Ditto, instar I larva (SCHLINGER & HALL, 1961). 94. *Praon exoletum*, ovarian egg (SCHLINGER & HALL, 1961). 95. *Diaeretiella rapae*, egg (ULLYETT, 1938). 96. *Aphidius avenae*, instar I larva hatching from egg (MACGILL, 1923). 97. *Diaeretiella rapae*, instar I larva, head showing mouth parts (ULLYETT, 1938). 98. Ditto, instar I larva (ULLYETT, 1938).

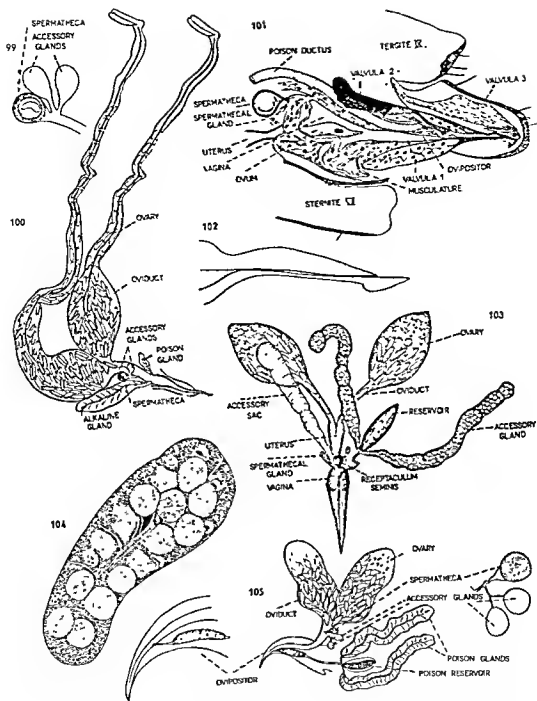


Fig. 99-105. 99. *Praon exoletum*, ♀ genitalia, accessory glands and spermatheca (SCHLINGER & HALL, 1960). 100. Ditto, ♀ genitalia (SCHLINGER & HALL, 1960). 101. *Diaeretiella rapae*, ♀ genitalia, longitudinal section (BROUSSAL, 1966). 102. *Praon exoletum*, ♀ genitalia, detail of ovipositor (SCHLINGER & HALL, 1960). 103. *Diaeretiella rapae*, ♀ genitalia (SEDLAG, 1957). 104. Ditto, ♀ genitalia, cross section through accessory gland (SEDLAG, 1957). 105. *Trioxyx complanatus*, ♀ genitalia (SCHLINGER & HALL, 1961).

found in the anterior region. The ovaries are continuous with the oviducts, which then unite into the common duct, *oviductus communis*. In the common duct, there are several openings: there the strongly sclerotized spermatheca opens whose duct is common for this and for two accessory glands. Further, there is the opening of the alkaline gland and, finally, an opening of a small poison or acid gland, which is a common duct of the poison gland and the poison reservoir. We should like to mention that there are various opinions as to the nomenclature and function of some parts of the accessory parts of the female reproductive system, on the poison gland namely (compare the figures).—The male genitalia consist of a pair of testes and a pair of large vesiculae seminales, which are connected each by a vas deferens. The testes are usually small, while the seminal vesicles are large.

REFERENCES. 21, 66, 79, 153, 155, 158, 159, 211, 309, 314, 438, 439, 460, 478, 497, 586, 591, 619, 679, 681, 684, 686, 696, 729, 730, 731, 734, 760, 762, 873, 915, 930, 937, 1003, 1005, 1018, 1020, 1046, 1062, 1069, 1095, 1096, 1107, 1111, 1121, 1125, 1127, 1158, 1189, 1214, 1223, 1231, 1237, 1238, 1239, 1247, 1284, 1295, 1299, 1305.

List of the Genera and Subgenera of the World

As it is apparent from the list, we prefer a more general classification of the group as to the genera. As we will mention in the phylogeny chapter, we do not accept any further subdivision of the aphidids into subfamilies, tribes, etc. for the time being, as our knowledge of the separate criteria is rather unequal.

Genus: *Acanthocaudus* SMITH, 1944.

Trioxys HALIDAY, 1833, subg. *Acanthocaudus* SMITH, 1944,

Ohio State Univ. Contr. Zoo. Ent., 6:85, 96.

Type species: *Trioxys* (*Acanthocaudus*) *tissoni* SMITH, 1944.

Genus: *Aclitus* FÖRSTER, 1862.

Aclitus FÖRSTER, 1862, Verh. Naturh. Ver. Preuss. Rheinl., 19:248.

Type species: *Aclitus obscuripennis* FÖRSTER, 1862.

Genus: *Aphidius* NEES, 1818.

Iucibus SCHRANK, 1802, Fauna boica, 2:315 (Rejected).

Type species: *Ichneumon aphidum* LINNAEUS, 1758.

Aphidius NEES, 1818, Nov. Acta Acad. L. C., p. 302.

Type species: *Bracon picipes* NEES, 1811 (Rejected).

Aphidius avenae HALIDAY, 1834, (design. by HINCKS, 1951).

Theracnion HOLMGREN, 1872, Öfvers. Svensk. Vet. Acad. Förh., 29(6):99.

Type species: *Theracnion arcticus* HOLMGREN, 1872.

Aphidius NEES, 1818, subg. *Enaphidius* MACKAUER, 1961, Beitr. Ent., 11:10.

Type species: *Aphidius pterocommae* ASHMEAD, 1900.

Genus: *Archaphidius* STARÝ & SCHLINGER, 1967.

Archaphidius STARÝ & SCHLINGER, 1967, Series ent. 3:30.

Type species: *Archaphidius greenideae* STARÝ & SCHLINGER, 1967.

Genus: *Areopraon* MACKAUER, 1959.

Areopraon MACKAUER, 1959, Beitr. Ent. 9:849-50.

Type species: *Praon lepelleyi* WATERSTON, 1926.

Genus: *Bioxys* STARÝ & SCHLINGER, 1967.

Bioxys STARÝ & SCHLINGER, 1967, Series ent. , 3:32.

Type species: *Bioxys japonicus* STARÝ & SCHLINGER, 1967.

Genus: *Boreogalba* MACKAUER, 1962.

Boreogalba MACKAUER, 1962, Canad. Ent., 94:1107-8.

Type species: *Boreogalba gladsfer* MACKAUER, 1962.

Genus: *Calaphidius* MACKAUER, 1961.

Calaphidius MACKAUER, 1961, Boll. Lab. Ent. Agr. Portici, 19:283.

Type species: *Calaphidius elegans* MACKAUER, 1961.

Genus: *Chaetopauesia* MACKAUER, 1967.

Chaetopauesia MACKAUER, 1967, Entomophaga, 12:141-2.

- Type species: *Chaetopauesia talis* MACKAUER, 1967.
 Genus: *Diaeretellus* STARÝ, 1960.
Diaeretellus STARÝ, 1960, Acta Soc. ent. Čechoslov., 57:243-4.
 Type species: *Aphidius ephippium* HALIDAY, 1834.
 Genus: *Diaeretiella* STARÝ, 1960.
Diaeretiella STARÝ, 1960, Acta Soc. ent. Čechoslov., 57:242-3.
 Type species: *Aphidius rapae* M'INTOSH, 1855.
 Genus: *Diaeretus* FÖRSTER, 1862.
Diaeretus FÖSTER, 1862, Verh. Naturh. Ver. Preuss. Rheinl., 19:249.
 Type species: *Aphidius leucopterus* HALIDAY, 1834.
 Genus: *Dyscritulus* HINCKS, 1943.
Dyscritus MARSHALL, 1896, in André, Spec. Hym. Europe d'Alg., 5:532, 617 (Preocc.).
 Type species: *Dyscritus planiceps* MARSHALL, 1896.
Dyscritulus HINCKS, 1943, Entomologist, London, 76:103, 224.
 Type species: *Dyscritus planiceps* MARSHALL, 1896.
 Genus: *Ephedrus* HALIDAY, 1833.
Aphidius NEES, 1818, subg. *Ephedrus* HALIDAY, 1833, Ent. Mag., 1:261, 485.
 Type species: *Bracon plagiator* NEES, 1811.
Elassus WESMAEL, 1835, Nouv. Mém. Acad. Sci. Bruxelles, 9:85.
 Type species: *Elassus parvicornis* WESMAEL, 1835.
 Subgenus: *Ephedrus* s. str.
Ephedrus HALIDAY, 1833, subg. *Ephedrus* s. str., STARÝ, 1958, Acta Faun. Ent. Mus. Nat. Praeae, 3:66-7.
 Type species: *Bracon plagiator* NEES, 1811.
 Subgenus: *Lysephedrus* STARÝ, 1958.
Ephedrus HALIDAY, 1833, subg. *Lysephedrus* STARÝ, 1958, Acta Faun. Ent. Mus. Nat. Praeae, 3:54.
 Type species: *Aphidius (Ephedrus) validus* HALIDAY, 1834.
 Genus: *Lipolexis* FÖRSTER, 1862.
Lipolexis FÖRSTER, 1862, Verh. Naturh. Ver. Preuss. Rheinl., 19:249.
 Type species: *Lipolexis gracilis* FÖRSTER, 1862.
Gynocryptus QUILIS, 1931, Eos, Madrid, 7:27-8.
 Type species: *Gynocryptus pictaini* QUILIS, 1931.
 Genus: *Lysaphidus* SMITH 1944.
Aphidius NEES, 1818, subg. *Lysaphidus* SMITH, 1944, Ohio State Univ. Contr. Zoo. Ent., 6:72.
 Type species: *Aphidius (Lysaphidus) adelocarinus* SMITH, 1944.
 Genus: *Lysiphlebia* STARÝ & SCHLINGER, 1967.
Lysiphlebia STARÝ & SCHLINGER, 1967, Setics ent. 3:68-9.
 Type species: *Lysiphlebus japonicus* ASHMEAD, 1906.
 Genus: *Lysiphlebus* FÖRSTER, 1862.
Lysiphlebus FÖRSTER, 1862, Verh. Naturh. Ver. Preuss. Rheinl., 19:248-50.
 Type species: *Aphidius* (= *Bracon*) *dissolutus* (NEES, 1811).
Aphidaria PROVANCHER, 1888, Addit. Corr. Faune ent. Canada, Hym., p. 396.
 Type species: *Aphidaria basilaris* PROVANCHER, 1888.
 Subgenus: *Adialytus* FÖRSTER, 1862.
Adialytus FÖRSTER, 1862, Verh. Naturh. Ver. Preuss. Rheinl., 19:249, 250.
 Type species: *Adialytus tenuis* FÖRSTER, 1862.
 Subgenus: *Lysiphlebus* s. str.
Lysiphlebus FÖRSTER, 1862, *Lysiphlebus* s. str., STARÝ, (in litt.).

- Type species: *Aphidius (Bracon) dissolutus* (NEES, 1811).
Lysiphlebus FÖRSTER, 1862, subg. *Platycyphus* MACKAUER, 1960, Beitr. Ent., 10: 590-1.
Type species: *Lysiphlebus (Platycyphus) macrocornis* MACKAUER, 1960.
Subgenus: *Phlebus* STARÝ (in litt.).
Lysiphlebus FÖRSTER, 1862, subg. *Phlebus* STARÝ, (in litt.).
Type species: *Aphidius fabarum* MARSHALL, 1896.
Genus: *Metaphidius* STARÝ & SEDLAG, 1959.
Aphidius NEES, 1818, subg. *Metaphidius* STARÝ & SEDLAG, 1959, D. ent. Z., N. F., 6:160-1.
Type species: *Aphidius (Metaphidius) trioxysformis* STARÝ & SEDLAG, 1959.
Genus: *Monoctonus* STARÝ, 1962.
Monoctonus STARÝ, 1962, Rev. d'Ent. de l'URSS, 41:876-7.
Type species: *Monoctonus pistaciicola* STARÝ, 1962.
Genus: *Monoctonus* HALIDAY, 1833.
Aphidius NEES, 1818, subg. *Monoctonus* HALIDAY, 1833, Ent. Mag., 1:261, 487.
Type species: *Aphidius (Monoctonus) caricis* HALIDAY, 1833.
Aphidleo RONDANI, 1848, Nuovi Ann. Sci. Nat. e Rend., Bologna, 2(9):14.
Type species: *Aphidius resolutus* NEES, 1834.
Subgenus: *Falcicomus* MACKAUER, 1959.
Monoctonus HALIDAY, 1833, subg. *Falcicomus* MACKAUER, 1959, Senck. biol., Frankfurt M., 40:180.
Type species: *Aphidius pseudoplatani* MARSHALL, 1896.
Subgenus: *Harkeria* CAMERON, 1900.
Harkeria CAMERON, 1900, Ann. Mag. Nat. Hist., 6:537.
Type species: *Harkeria rufa* CAMERON, 1900.
Subgenus: *Monoctonus* s. str.
Monoctonus HALIDAY, 1833, *Monoctonus* s. str., STARÝ, 1959, Acta Soc. ent. Českoslov., 59:241-2.
Type species: *Aphidius (Monoctonus) caricis* HALIDAY, 1833.
Subgenus: *Paramonoctonus* STARÝ, 1959.
Monoctonus HALIDAY, 1833, subg. *Paramonoctonus* STARÝ, 1959, Acta Soc. ent. Českoslov., 56:238-9.
Type species: *Monoctonus (Paramonoctonus) angustivalvus* STARÝ, 1959.
Genus: *Paralipsis* FÖRSTER, 1862.
Paralipsis FÖRSTER, 1862, Verh. Naturh. Verh. Preuss. Rheinl., 19:248.
Type species: *Aphidius euervis* NEES, 1834.
Myrmecobosca MANEVAL, 1940, Bull. Soc. Linn. Lyon, 9:9.
Type species: *Myrmecobosca mandibularis* MANEVAL, 1940.
Genus: *Paesia* QUILIS M.P., 1931.
Paesia QUILIS, 1931, Eos, Madrid, 7:67-9.
Type species: *Paesia albuferensis* QUILIS, 1931.
Aphidius NEES, 1818, subg. *Paraphidius* STARÝ, 1958, Acta Faun. Ent. Mus. Nat. Pragae, 3:56, 91.
Type species: *Aphidius californicus* ASHMEAD, 1888.
Genus: *Praon* HALIDAY, 1833.
Aphidius NEES, 1818, subg. *Praon* HALIDAY, 1833, Ent. Mag., 1:483.
Type species: *Bracon exoletus* NEES, 1811.
Bracon NEES, 1811, subg. *Achoristus* RATZBURG, 1852, Ichn. d. Forstins., 3:31-2.
Type species: *Bracon (Achoristus) aphidiiformis* RATZBURG, 1852.
Aphidaria PROVANCHER, 1886, Add. Faun. Canad. Hym., p. 151.
Type species: *Aphidaria simulans* PROVANCHER, 1886.

- Genus: *Protaphidius* ASHMEAD, 1900.
Coelonotus FÖRSTER, 1862, Verh. Naturh. Ver. Preuss. Rheinl., 19:248 (Preocc.)
 Type species: *Coelonotus rufus* FÖRSTER, 1862.
Protaphidius ASHMEAD, 1900, Canad. Ent., 32:368.
 Type species: *Coelonotus rufus* FÖRSTER, 1862.
Menozzia GOIDANICH, 1934, Boll. Lab. ent. Bologna, 6:217-29.
 Type species: *Menozzia formicaria* GOIDANICH, 1934.
- Genus: *Pseudephedrus* STARÝ, (in litt.)
Pseudephedrus STARÝ, (in litt.)
 Type species: *Pseudephedrus neotropicalis* STARÝ, (in litt.)
- Genus: *Tanytrichophorus* MACKAUER, 1961.
Tanytrichophorus MACKAUER, 1961, Boll. Lab. Ent. Agr. Portici, 19:271-2.
 Type species: *Tanytrichophorus petiolaris* MACKAUER, 1961.
- Genus: *Toxares* HALIDAY, 1840.
Aphidius NEES, 1818, subg. *Trionyx* HALIDAY, 1833, Ent. Mag., 1:487 (Preocc.).
 Type species: *Aphidius (Trionyx) deltiger* HALIDAY, 1833.
Toxares HALIDAY, 1840, in WESTWOOD, 1840, Introd. Mod. Classif. Insects, 2: Synops., p. 65.
 Type species: *Aphidius (Trionyx) deltiger* HALIDAY, 1833.
- Genus: *Trioxys* HALIDAY, 1833.
Aphidius NEES, 1818, subg. *Trionyx* HALIDAY, 1833, Ent. Mag., 1:261-488.
 Type species: *Aphidius cirsii* CURTIS, 1831.
Misaphidius RONDANI, 1877, Boll. Soc. Ent. Ital., 9:185.
 Type species: *Misaphidius aphidiperda* RONDANI, 1877.
Neuropenes PROVANCHER, 1886, Add. Faun. Canad. Hym., p. 151, 153.
 Type species: *Neuropenes ovalis* PROVANCHER, 1886.
- Subgenus: *Betuloxys* MACKAUER, 1960.
Trioxys HALIDAY, 1833, subg. *Betuloxys* MACKAUER, 1960, Beitr. Ent., 10:139.
 Type species: *Trioxys compressicornis* RUTHIE, 1859.
- Subgenus: *Binodoxys* MACKAUER, 1960.
Trioxys HALIDAY, 1833, subg. *Binodoxys* MACKAUER, 1960, Beitr. Ent., 10:141.
 Type species: *Aphidius (Trioxys) angelicae* HALIDAY, 1833.
- Subgenus: *Fissicaudus* STARÝ & SCHLINGER, 1967.
Trioxys HALIDAY, 1833, subg. *Fissicaudus* STARÝ & SCHLINGER, 1967, Series ent., 3:122.
 Type species: *Trioxys (Binodoxys) confucius* MACKAUER, 1962.
- Subgenus: *Pectoxys* MACKAUER, 1960.
Trioxys HALIDAY, 1833, subg. *Pectoxys* MACKAUER, 1960, Beitr. Ent., 10:154-5.
 Type species: *Trioxys (Trioxys) macroceratus* MACKAUER, 1960.
- Subgenus: *Trioxys* s. str.
Trioxys HALIDAY, 1833, subg. *Trioxys* s. str., MACKAUER, 1959, Beitr. Ent., 9:149.
 Type species: *Aphidius cirsii* CURTIS, 1831.
- Genus: *Xenostigmus* SMITH, 1944.
Aphidius NEES, 1818, subg. *Xenostigmus* SMITH, 1944, Ohio State Univ. Contr. Zoo. Ent., 6:35-6.
 Type species: *Aphidius bifasciatus* ASHMEAD, 1891.

Key to the Genera and Subgenera of the World

- 1 Wings fully developed 2
 - Apterous *Diaretellus* STARÝ
- 2 (1) Median vein developed throughout, separating radial cell 1 from median cell (Figs. 107, 115) 3
 - Median vein effaced frontally or entirely, radial cell 1 and median cell 1 confluent; venation often reduced behind basal vein (Figs. 110, 112, 161, 170) 7
- 3 (2) Interradial veins effaced (Figs. 115, 135) 4
 - Both interr radial veins developed (Fig. 107) 6
- 4 (3) Radial vein developed throughout, pterostigmal cell (Fig. 135) almost complete. Median vein strongly sclerotized almost to wing apex. Pupation inside mummified aphid. *Pseudephedrus* STARÝ
 - Radial vein shorter, never reaching wing margin, pterostigmal cell distinctly incomplete. Median vein more or less colourless in its fore portion (Fig. 115). Pupation inside or under mummified aphid 5
- 5 (4) Propodeum smooth. Ovipositor sheaths sparsely haired (Fig. 174). Pupation under parasitized aphid in a separate cocoon. *Praon* HALIDAY
 - Propodeum more or less distinctly areolated (Fig. 134). Ovipositor sheaths densely haired (Fig. 174). Pupation inside mummified aphid *Areopraon* MACRAUER
- 6 (3) Ovipositor sheaths and ovipositor straight or slightly curved downwards (Figs. 126, 163). Antennae 11-segmented. Abdomen lanceolate. *Ephedrus* HALIDAY
 - a Propodeum coarsely irregularly and deeply rugose. (Fig. 137). Ovipositor sheaths densely pubescent. (Fig. 126) *Lysephedrus* STARÝ
 - Propodeum regularly areolated, discs of areolae smooth to almost smooth, sometimes slightly sculptured near the carinae (Fig. 124). Ovipositor sheaths with scattered hairs (Fig. 163) *Ephedrus* s. str.
 - Ovipositor sheaths curved downwards, rather broadened, deltoid and trifid at extremity (Fig. 141). Ovipositor curved downwards. Antennae 18-segmented. Abdomen rounded. *Toxares* HALIDAY
- 7 (2) Radial and median cells confluent, distinctly completed by second interr radial vein along their external margin (second interr radial vein sometimes nearly colourless but distinct (Figs. 112, 169, 170) 8
 - Radial and median cells confluent, open, not completed by interr radial vein 2 along their external margin (Figs. 110, 161, 176) 19
- 8 (7) Pterostigmal cell distinctly complete (Fig. 117) 9
 - Pterostigmal cell incomplete (Figs. 112, 170) 10
- 9 (8) Eyes small, (Fig. 122). Antennae moniliform. Notaulices distinct at base as slight rugosities. Propodeum smooth. Abdomen rounded. Tergite 1 transverse. *Aclitus* FÖRSTER

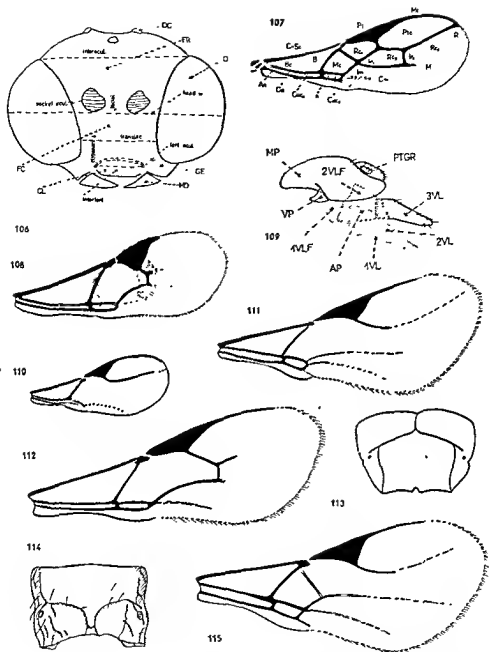


Fig. 106-115. Note: The figures 106-178 were compiled from the following papers: STARÝ, 1966, 1968, STARÝ & SCHLINGER, 1967, except where otherwise stated.

106. Morphology and nomenclature of head. FC - facies, CL - clypeus, MD - mandible, GE - gena, O - eye, FR - frons, OC - ocellus, interocul. - interocular line, socket ocul. - socketocular line, facial w. - head width, transfac. - transfacial line, tent. ocul. - tentono-ocular line, clypeoant. - clypeoantennal line, intertent. - intertentorial line. 107 Nomenclature of wing venation, *Ephedrus* sp. Pt - pterostigma, Mt - meracarpus, C - costal vein, Se - subcostal vein, B - basal vein, Be - basal cell, An - anal vein, Cu - cubital vein, $Cuc_{1,2}$ - cubital cell 1, 2, n - nervulus, $R_{1,2,3}$ - radial cell 1, 2, 3, $Ir_{1,2}$ - interradial vein 1, 2, Mc - median cell, Im - inter-median vein, R - radial vein, M - median vein, Ptc - pterostigmal cell. 108. *Xenostigmus bifasciatus*, fore wing. 109 Nomenclature of ♀ genitalia, lateral view. MP - median

prong of IXth tergite, PTGR – proctiger, VLF – valvifer (1, 2), VL – valvula (1, 2, 3), VP – ventral prong of IXth tergite, AP – anterior prong of 2nd valvula. 110. *Lipolexis gracilis*, fore wing. 111. *Dyscritulus planiceps*, fore wing. 112. *Aphidius rosae*, fore wing. 113. *Paesia picta*, propodeum. 114. *Archaphidius greenideae*, propodeum. 115. *Praon* sp., fore wing.

- Eyes large. Antennae filiform. Notaulices effaced. Propodeum partially carinated. Abdomen lanceolate. Tergite 1 distinctly longer than wide at spiracles.

Archaphidius STARÝ & SCHLINGER

- 10 (8) Confluent radial and median cells distinctly separated on lower margin by fused intermedian and median vein (Fig. 112). 11

- Confluent radial and median cells on the lower margin open—the rest of median vein visible only under the second interradiial vein (Fig. 170). 17

- 11 (10) Abdominal segments beginning with the 4th remarkably tubiform and telescopic (Fig. 152) *Protaphidius* ASHMEAD

- Abdominal segments of normal shape, abdomen lanceolate or rounded 12

- 12 (11) Ovipositor sheaths slightly curved upwards 13

- Ovipositor sheaths curved downwards, ploughshare-shaped, or slender, gradually narrowing to the apex (Figs. 151, 157). (Note: wing venation variable).

Monoctonus HALIDAY

- a Propodeum distinctly areolated (Fig. 120). Ovipositor sheaths ploughshare-shaped (Fig. 151), or slender and gradually narrowing to the apex (Fig. 133). c

- Propodeum with two divergent carinae in lower portion, sometimes with feeble rugose markings as remainder of central areola. Ovipositor sheaths long and slender, only slightly dilated in the centre and narrowing to the apex (Fig. 157). b

- b (a) Antennae 14–15-segmented. Propodeum smooth, with two divergent carinae in lower part (Fig. 164). Tergite 1 with prominent spiracular tubercles (Fig. 140), almost twice as long as wide at spiracles *Paramonotonus* STARÝ

- Antennae 16-segmented. Propodeum slightly granulate, with two divergent carinae in lower portion and small rugosities as remainders of central areola. Tergite 1 with poorly prominent spiracular tubercles, almost parallel-sided, almost 3 times as long as wide at spiracles *Harkeria* CAMERON

- c (a) Ovipositor sheaths stout, ploughshare-shaped (Fig. 151).

Monoctonus s. str.

- Ovipositor sheaths slender, gradually narrowing to the apex (Fig. 133)

Falcitonus MACKAUER

- 13 (12) Metacarp shorter than width of pterostigma (Fig. 108). *Xenostigmus* SMITH

- Metacarp longer than width of pterostigma (Fig. 112). 14

- 14 (13) Carinae on propodeum forming large wide pentagonal areola (sometimes poorly visible in the longitudinal portion) (Fig. 113). 15

- Carinae on propodeum forming very narrow, small, central areola (Fig. 162).

Aphidius NEES

- 15 (14) Tergite 7 with small tubiform prong at base (Fig. 121).

Metaphidius STARÝ & SEDLAG

- Tergite 7 without small tubiform prong at base. 16

- 16 (15) Ovipositor sheaths with sparse hairs

Paesia QUILIS

- Ovipositor sheaths densely pubescent

Chaetopaesia MACKAUER

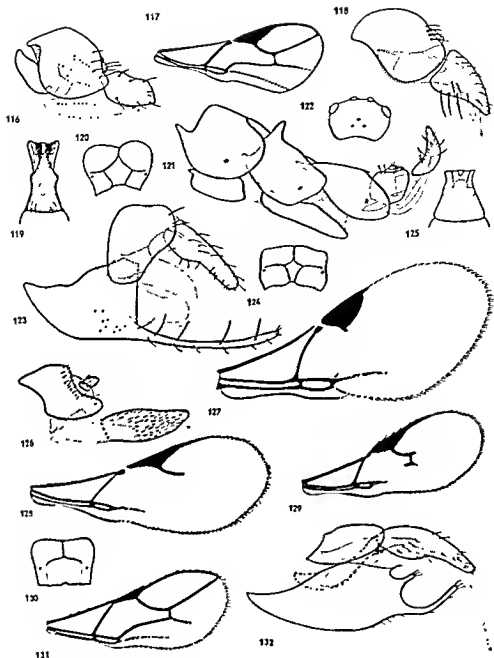


Fig. 116-132. 116. *Lysaphidus arvensis*, ♀ genitalia. 117. *Archaphidus greenideae*, fore wing. 118. *Monotonus putziasicola*, ♀ genitalia. 119. *Lymphlebus salicaphis*, tergite 1. 120. *Monotonus crepidis*, propodeum. 121. *Metaphidius aterrimus*, apex of abdomen. 122. *Aclous obscuripennis*, head from above. 123. *Trioxys angelicae*, ♀ genitalia. 124. *Ephedrus iramola*, propodeum. 125. *Lymphlebus fabarum*, tergite 1. 126. *Ephedrus validus*, ♀ genitalia. 127. *Paraphus enervis*, fore wing. 128. *Monotonus angustulus*, fore wing (variation). 129. *Lysaphidus erymus*, fore wing. 130. *Diacretus leuopterus*, propodeum. 131. *Aclous obscuripennis*, fore wing. 132. *Anthracocaudus tisseroti*, ♀ genitalia (SMITH, 1944).

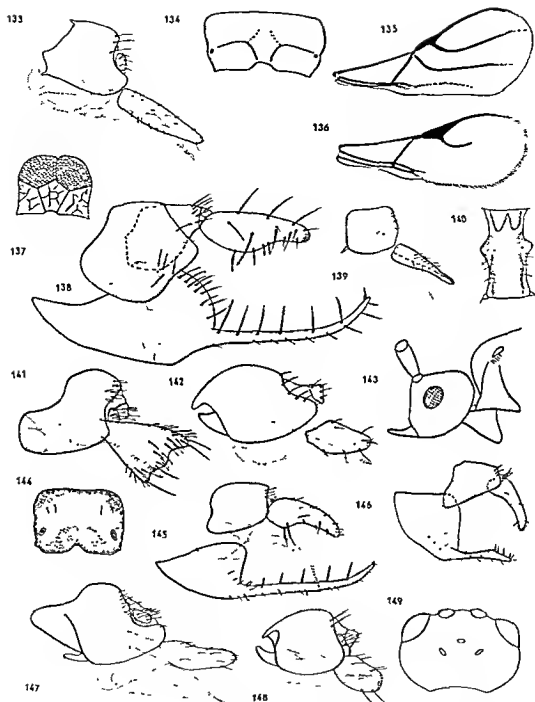


Fig. 133-149. 133. *Monoctonus pseudoplatani*, ♀ genitalia. 134. *Areopraon lepellei*, propodeum. 135. *Pseudephedrus neotropialis*, fore wing. 136. *Lysiphlebus salicaphis*, fore wing. 137. *Ephedrus validus*, propodeum. 138. *Trioxys centanrae*, ♀ genitalia. 139. *Lipolexis gracilis*, ♀ genitalia. 140. *Monoctonus angustivalvus*, tergite 1. 141. *Toxares deltiger*, ♀ genitalia. 142. *Lysiphlebia japonica*, ♀ genitalia. 143. *Paralipsis eikoe*, head and part of the thorax, lateral view (YASUMATSU, 1951). 144. *Lysiphlebus* sp., propodeum. 145. *Trioxys pannonicus*, ♀ genitalia. 146. *Trioxys hortorum*, ♀ genitalia. 147. *Praon volucre*, ♀ genitalia. 148. *Diactetiella rapae*, ♀ genitalia. 149. *Dyscritulus planiceps*, head from above.

- 17 (10) Tergite 1 with more or less developed central tubercle only, without central carina or coarse rugosities (Figs. 119, 125, 144). Tentorio-ocular line almost or equal to intertentorial line. *Lysiphlebus* FÖRSTER
- a Flagellar segments distinctly longer than wide. Antennae 12-14-segmented. b
- Flagellar segments distinctly square. Antennae 15-16-segmented *Lysiphlebus* s. str.
- b (a) The rest of cubital and median vein distinct (Fig. 170). Interradial vein 2 distinct, somewhat colourless. Tergite 1 widely triangular (Fig. 125) *Phlebus* STARÝ
- Only radial vein developed, the rest of cubital and median vein similarly as interradial vein 2 absent (Fig. 136). Tergite 1 slender, somewhat dilating to the apex (Fig. 119) *Adalytus* FÖRSTER
- Tergite 1 with more or less distinct central carina, more or less rugose. Tentorio-ocular line equal or shorter than intertentorial line. 18
- 18 (17) Tentorio-ocular line equal to intertentorial line. Anterior prong of valvulae 2 normal (Fig. 142). *Lysiphlebia* STARÝ & SCHLINGER
- Tentorio-ocular line distinctly shorter than intertentorial line, usually equal to 1/3. Anterior prong of valvulae 2 large and appearing flat from side (Fig. 116). *Lysaphidus* SMITH
- 19 (7) Radial vein pointlike. Pterostigma large, triangular, strongly sclerotized (Fig. 127, 165). Legs strong. *Paralipsis* FÖRSTER
- Radial vein distinctly developed, always longer, never pointlike. Legs normal 20
- 20 (19) Ovipositor sheaths curved downwards, terminal abdominal sternite sometimes with 1-2 prongs (Figs. 145, 155, 139) 21
- Ovipositor sheaths straight or slightly curved upwards, terminal abdominal sternite without posterior prongs (Fig. 148, 158) 27
- 21 (20) Terminal abdominal sternite with 2-1 longer or shorter prongs (Figs. 145, 155) 22
- Terminal abdominal sternite without prongs 24
- 22 (21) Terminal abdominal sternite with 1 upward curved prong (Fig. 155). *Bioxys* STARÝ & SCHLINGER
- Terminal abdominal sternite with 2 upward curved to nearly straight prongs (Figs. 145, 166) 23
- 23 (22) Posterior prongs on terminal abdominal sternite with accessory prongs (Fig. 132) *Acanthocaudus* SMITH
- Posterior prongs on terminal abdominal sternite simple (Fig. 143). *Trioxys* HALIDAY
- a Tergite 1 with primary (- spiracular) and secondary tubercles (Fig. 177), the latter sometimes poorly visible being almost fused with primary tubercles.. b
- Tergite 1 with primary tubercles only c
- b (a) Prongs of the last sternite beginning at the apex of sternite (Fig. 123) *Binodoxys* MACKAUER
- Prongs of the last sternite beginning near the base of sternite (Fig. 168) *Fissicaudus* STARÝ & SCHLINGER
- c (a) Prongs with dilated and strongly differentiated apical portion, with several stout bristles dilated at the base (Fig. 146) *Betuloxys* MACKAUER
- Prongs slightly curved to nearly straight, without differentiated apical portion (Fig. 143) d
- d (c) Ovipositor sheaths normal, apical bristles normal, dilated at the base. Primary tubercles situated at the first third. Prongs of variable length (Fig. 143). *Trioxys* s. str.

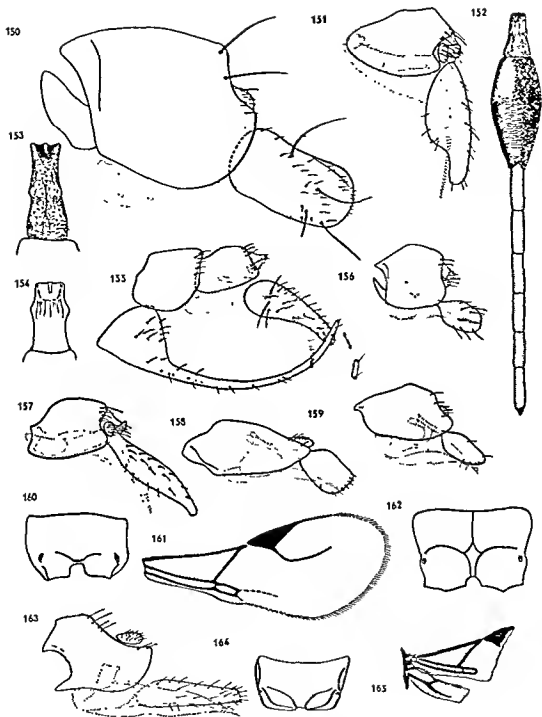


Fig. 150-165. 150. *Pauesia abietis*, ♀ genitalia. 151. *Monoctonus erepidis*, ♀ genitalia. 152. *Protaphidius wismannii*, abdomen (GOIDANICH, 1934). 153. *Lysiphlebia japonica*, tergite 1. 154. *Trioxys auctus*, tergite 1. 155. *Bioxys japonicus*, ♀ genitalia. 156. *Diaeretellus ephippium*, ♀ genitalia. 157. *Monoctonus angustivalvus*, ♀ genitalia. 158. *Diaeretus leucop-terus*, ♀ genitalia. 160. *Lysiphlebus dissolutus*, propodeum. 161. *Trioxys angelicae*, fore wing. 162. *Aphidius rosae*, propodeum. 163. *Ephedrus plagiator*, ♀ genitalia. 164. *Monoc-tonus angustivalvus*, propodeum. 165. *Paralipsis enervis*, wing bubbled by ants (MANEVAL, 1940).

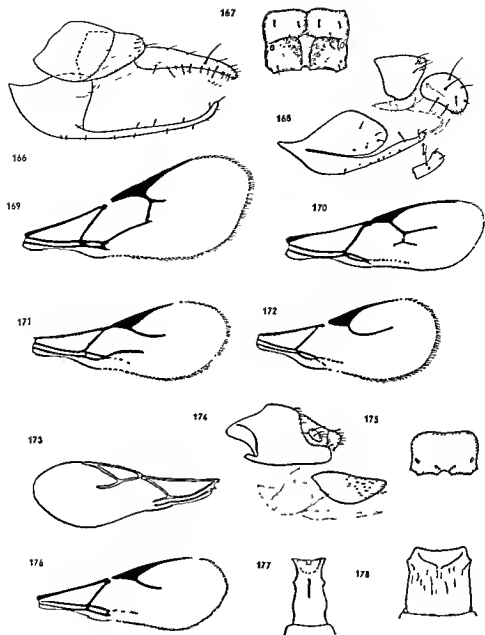


Fig. 166-178. 166. *Trioxys macroceratus*, ♀ genitalia. 167. *Lysiphlebia japonica*, propodeum. 168. *Trioxys confucius*, ♀ genitalia. 169. *Monoctonus angustivalvus*, fore wing. 170. *Lysiphlebus melandriicola*, fore wing. 171. *Diaeretellus ephippium*, fore wing. 172. *Diaeretus leucopterus*, fore wing. 173. *Boreogalba gladifer*, fore wing (after MACKAUER). 174. *Areopraon lepelleys*, ♀ genitalia. 175. *Lysiphlebus salicaphus*, propodeum. 176. *Diaeretiella rapae*, fore wing. 177. *Trioxys angelicar*, tergite 1. 178. *Monoctonia pistaciaecola*, tergite 1.

- Ovipositor sheaths rather long, with stout brush-like bristles at the inner side (Fig. 166). Prongs remarkably long, without apical bristles. Primary tubercles near the mid-line or at the first third of the tergite *Pectoxys* MACKAUER
 - 24 (21) Radial vein longer than $\frac{2}{3}$ of its possible length so that pterostigmal cell nearly complete. Ovipositor sheaths slightly curved downwards, their upper part more strongly sclerotized (Fig. 139). *Lipolexis* FÖRSTER
 - Radial vein never longer than $\frac{2}{3}$ of its possible length; pterostigmal cell distinctly incomplete. Ovipositor sheaths slightly curved downwards, more or less ploughshare-shaped, or clawed or slender 25
 - 25 (24) Tergite 1 always longer than wide at spiracles. Ovipositor sheaths triangular, ploughshare-shaped, or slender, gradually narrowing to the apex 26
 - Tergite 1 square (Fig. 178). Ovipositor sheaths triangular, clawed (Fig. 118). *Monoctonus* STARÝ
 - 26 (25) Median and intermedian vein at least partly distinct see: *Monoctonus* HALIDAY
 - Median and intermedian vein entirely effaced (Fig. 173) *Borcogalba* MACKAUER
 - 27 (20) Notaulices entirely effaced. Propodeum with more or less distinct wide central areola (Fig. 130). *Diaeretus* FÖRSTER
 - Notaulices at least at the base distinct 28
 - 28 (27) Propodeum distinctly areolated, with small central areola 29
 - Propodeum smooth or with 2 divergent carinae in the lower part see: *Lysiphlebus* FÖRSTER
 - 29 (28) Head nearly square (Fig. 149). Notaulices deep and distinct throughout. Pupation under parasitized aphid in a separate cocoon *Dyseritulus* HINCKS
 - Head transverse. Notaulices more or less deep but distinct at the ascendent part only 30
 - 30 (29) Intermedian vein (fused with part of median vein) entirely effaced (Fig. 176). *Diaeretiella* STARÝ
 - Intermedian vein (fused with part of median vein) distinct, somewhat less coloured than the radial vein (Fig. 171). Sometimes ♀♀ wingless *Diaeretellus* STARÝ
- Note: The following genera are not included in the key—*Calaphidius* MACKAUER, *Tanytrichophorus* MACKAUER

Bionomics and Life-History

Development

EMBRYONIC DEVELOPMENT. The embryonic development of the aphidids* manifests rather similar general features as far as the intermediate and late embryonic development stages are concerned. Striking differences were observed in the early embryogeny between two generic groups. For this reason we have decided to deal with the embryonic development in an *Ephedrus* species in more detail, the differences known to occur in other genera and species being mentioned as an addition.

Ephedrus plagiator (partially after IVANOVA KASAS 1961). The eggs are alecithal, the plasma appears to be homogeneous. The external cover is formed by the chorion. Oosoma is situated at the hind end of the egg (Fig. 180).

In newly deposited eggs the nucleus cannot be differentiated. After initiation of cleavage the nuclei have the form of rounded light small bladders. Although there is a lack of yolk and the egg is small, the cleavage is typically partial. At the stage of four cleavage nuclei the free space between the egg surface and chorion disappears (Fig. 192).

Then there appears a boundary that separates the central plasma with differentiated nuclei from the blastoderm. As the number of cells gradually becomes higher, the blastoderm becomes irregularly two-layered. Then the blastoderm differentiates into an upper layer, which is characterized by lighter nuclei that are situated less compactly, and a lower layer, whose nuclei are situated more compactly and are elongated perpendicularly to the surface of the egg. From the upper layer the serosa develops, from the lower layer the embryo develops: thus, the serosa develops through delamination. After the development of the embryonic envelope the cells or rudiments of the reproductive organs are situated beneath the serosa (Fig. 193).

Further, the embryo increases in length. Along the longitudinal axis a narrow tubiform space develops, in which the degenerative remnants of plasma and yolk nuclei may be found (Fig. 193). On a cross section it can be observed that the embryonic blastoderm does not form a continuous layer, but it is interrupted at one side and is furrow-like (Fig. 190). Then, the embryonic envelope of the embryo extends in width, becomes more spacious (Fig. 190) and the borders of the mentioned furrow appear to expand (Fig. 191). At this stage, the embryo has the shape of a germ band, but differs in that it does not lie on the yolk and its borders do not pass into amnion, as both yolk and amnion are lacking. In a corresponding manner, the side to which the open part of the furrow is directed must be considered as the dorsal side, and the opposite one as the ventral side.

In a cross-section of the germ band (Fig. 191) three areas may be differentiated,

* The author is indebted to Prof. Dr. E. TREMBLAY for many valuable notes regarding the development of the aphidids.

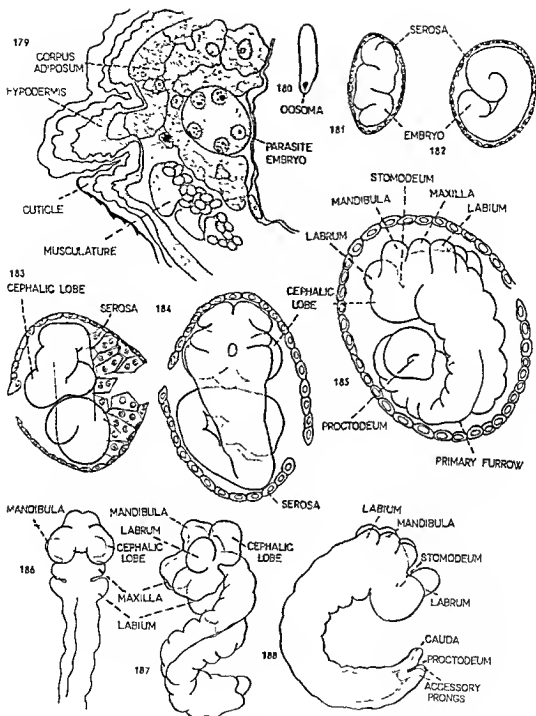


Fig. 179-188. 179. *Ephedrus plagiator*. Egg in tissues of an aphid. 180. Egg at the beginning of cleavage. 181. Irregular curving of embryo. 182. Spirally curved embryo. 183. Development of cephalic lobes. 184. Segmentation. 185. Initial stage of shortening. 186. Embryo taken out of the envelope, fore portion. 187. Embryo taken out of the envelope, at the period of shortening. 188. Embryo taken out of the envelope, advanced stage (all figures redrawn from IVANOVA KASAS 1961).

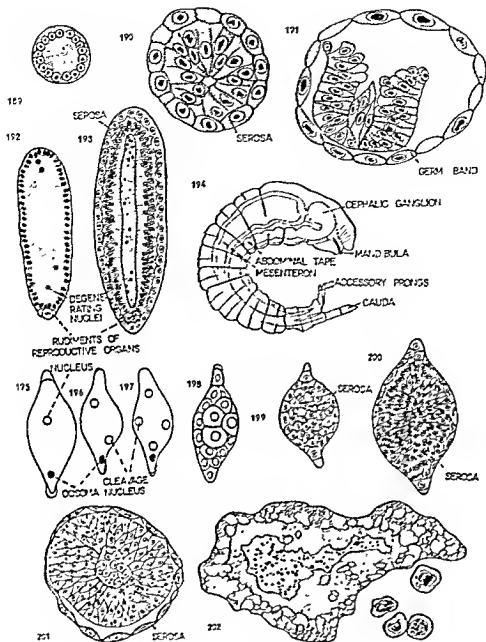


Fig. 189-202. 189 *Ephedrus plagiator*. Embryo at the end of segmentation stage; transversal section. 190. Ditto, after the development of serosa. 191. Ditto, stage of germ band. 192. Egg at the end of cleavage. 193. Embryo with differentiated blastoderm and serosa. 194. First instar larva (all figures drawn from IVANOVA KASAS 1961). 195-198. Early stages of embryonic development of *Aphidius* sp. 195. Egg before cleavage. 196. Stage of two cleavage nuclei. 197. Stage of four cleavage nuclei. 198. Total cleavage. 199-201. Development of embryonic envelope, *Aphidius* sp. 202. Section. 202. 'Giant cells' of various stages (all figures redrawn from IVANOVA KASAS 1961).

which differ in the distribution of cells. The lateral sides of the band are composed of two epithelial layers, which are well limited externally and internally, consisting of high cylindrical cells, which are well compacted altogether. In the median portion the germ band is well differentiated only externally, and the cells which form it are irregularly elongated into the cavity of the furrow. Obviously, there the process of differentiation of the mesoderm begins.

At this period, approximately after 24 hours from egg-deposition, the embryo (and envelope) becomes distinctly increased in size. The embryo for example becomes elongated; it is not elongated under the envelope, but it forms irregular bends (Fig. 181) and later it is loop-shaped (Figs. 182, 183) or slightly spiral-shaped (Fig. 185).

Then the lateral portions of the germ band become confluent at the dorsal side, so that the embryo is sausage-shaped. The fore portion of the embryo forms a transversal enlargement—the cephalic lobes (Figs. 183, 184, 185)—and along the whole length of the embryo the slight impressions—the first signs of segmentation—appear. The cephalic lobes gradually become massive. Among them, there appears an unpaired lobe, which is slightly ventrally directed and represents the origin of the labrum (Fig. 185); near its basis, a deep cylindrical impression may be observed, the stomodeum (Fig. 185). In the following three segments the paired ventral-lateral lobes develop—the rudiments of mandibles, maxillae, and labium (Fig. 185). In the hind end of the embryo a slight enlargement may be observed, on which the impression of proctodeum can be distinguished.

The further development of the embryo is connected with its enlargement. For this reason, the proportions of the body change and the embryo appears to be shorter. Segmentation of the body becomes well distinguishable. At the hind end, the unpaired cauda and two perpendicular ventral prongs can be seen (Fig. 188). The relative dimensions of the mouth portions diminish. Gradually, the embryo exhibits the forms of the future first instar larva, but because of blastokinetic movement it is situated turned the other way round, with its ventral part outside (compare Figs. 188 and 194).

During embryonic development the embryo rather increases in dimensions, the stage figured (Fig. 188) is 300times larger and the instar I. larva (Fig. 194) 400times larger than the deposited egg (IVANOVA KASAS, 1961).

The eggs of the aphidids are of monoembryonic type, as only a single larva is produced from an individual egg.

Remarkable differences from the above mentioned development of *Ephedrus*-species can be found to occur in the early embryogeny of other groups such as *Aphidius* and more or less related genera (*Diaeretiella*, *Lysiphlebus*) (IVANOVA KASAS 1961, TREMBLAY 1966) (Figs. 180-202, 203-213.) In *Ephedrus* the development of the embryonic envelope occurs later than in *Aphidius*; in *Ephedrus*, the envelope originates through delamination of the blastoderm, while in *Aphidius* it derives from a differentiation of blastomeres. Further, the greater number of cells in the serosa of *Ephedrus* conditions a less elongation of the cells and this enables the embryo to occur in a more free manner inside, there being consequently not such a great bending of the embryo as in *Aphidius*. However, the most important fact is in that there are less palingenetic peculiarities in *Aphidius*, for example, the cleavage in *Aphidius* becomes total rather soon, and this is connected with the lack of the blastoderm stage, lack of homologue of yolk nuclei and the germ band does not develop at all. Further, the manner of development of the embryonic envelope is more changed in *Aphidius* and this process may be observed in an earlier period; this is believed to have an adaptive significance as the serosa has rather important functions. Consequently,

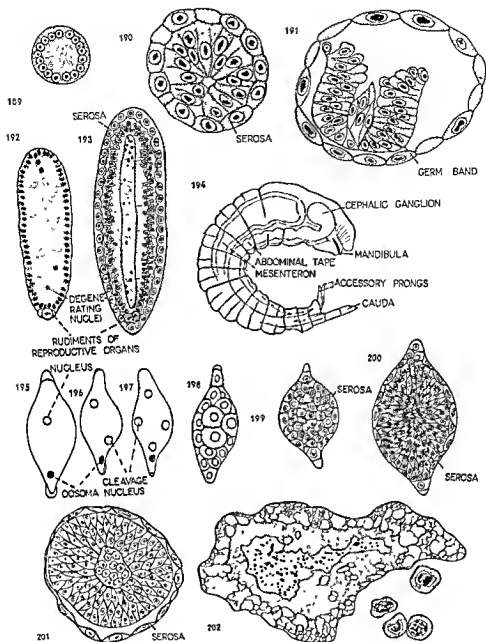


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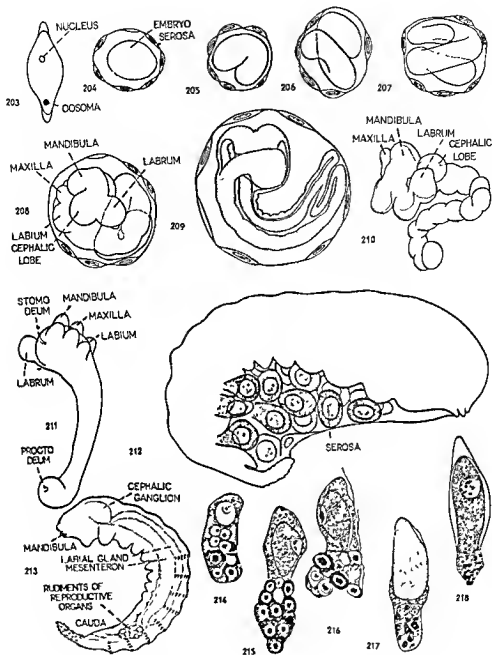


Fig. 203-218. 203-209. *Aphidius* sp. Development and changes of the embryo. Successive developmental stages. 210-211. Embryo taken out of the envelope, advanced stage. 212. First instar larva before hatching. 213 First instar larva (all figures redrawn from IVANOVA KASAS 1961). 214-218. Nutritive cells of an egg (*Diacretella rapae*), 214. the youngest egg, 218. the oldest egg (redrawn from SEDLAG 1957).

Aphidius is more adapted to the parasitic conditions of embryonic development and it is more deviated from the more general type of insect evolution than the relatively more primitive *Ephedrus*. Nevertheless, another viewpoint can be applied with respect to the development of adaptation. The comparison of the embryonic development of *Ephedrus* and *Aphidius* shows that the rapidity of morphological evolution is not coincident with the evolution of physiological adaptation; in this case the ability of the parasite embryo to feed on the host is rather important as it may be expressed quantitatively during the embryonic development: although *Ephedrus* is evolutionarily more ancient as to its morphology than *Aphidius*, it is more progressive physiologically, as a greater enlargement of the parasite embryo during embryonic development may be observed in *Ephedrus* (after IVANOVA KASAS 1961).

POSTEMBRYONIC DEVELOPMENT. When the embryonic development is completed, the larva uses its mandibles and causes a rupture of the embryonal envelope and hatches, then laying freely in the host body cavity (Fig. 96).

The further fate of the serosal cells is rather important. After the larva has hatched, numerous pieces of the broken serosa are found next to the larva, each of them varying in size and number of nuclei. These fragments of the serosa then change their size in rounding off, they grow very quickly and fare, rich in nutritive substances (glycogen, protein, fat). These substances then serve, in a similar way as the aphid body fluids and tissues, as food for the parasite larva and this is why their cytoplasm becomes more and more vacuolated as the parasite larva develops, the size of degenerating mass increasing (Fig. 202).

The serosal cells, which are generally known as "giant cells", can develop if the parasite larva dies and they themselves cause the death of the host (OGLOBLIN 1942, IVANOVA KASAS 1961, RUBTZOVA 1966, TREMBLAY 1966).

- **LARVA.** 1. The first instar larva mostly feeds by liquid food ingestion. The rather prominent and acute mandibles have no gnawing function: their use may be to puncture membranous tissue in order to permit discharge of liquid or semiliquid contents. The larva diffuses some cytolytic excretion into the host body fluids and this excretion influences the young embryos and ova of the host, while the ovaries, mature embryos, etc., are not affected (see: influence of parasite on the host). Adipose tissue is also influenced by the excretion in a similar manner.

The first instar larva moves in using either a body contracting and expansion, or a caudal prong and even the setae on body segments may be useful (see: SCHLINGER & HALL 1960).

2. The Instar II. larva is also mandibulate, but it feeds in an osmotic way in a similar manner to the instar I. larva.

3. The Instar III. larva is emandibulate and feeds osmotically similarly as the previous instar larvae. Likewise, it does not cause any injury to the vital organs of the host, and feeds on the body fluids of the host, but, naturally, the number of injured aphid embryos, adipose cells and giant cells is correspondingly higher.

There are various observations on the manner of feeding of separate instar larvae (e.g. compare SPENCER 1926, TREMBLAY 1966, and SCHLINGER & HALL 1960).

4. The Instar IV. larva is mandibulate and uses its mandibles to cause injury to the vital organs of the host and completely consumes the inside of the aphid, which is killed in consequence: after the content of the abdomen is consumed, the larva begins to feed on the inside of the thorax and head and it was even observed to suck food material from the host's legs; after the whole content of the host body is consumed, the larva scrapes the host body integument by labiostipital sclerome to consume really everything (see: SCHLINGER & HALL 1960). Thus, the larva remains

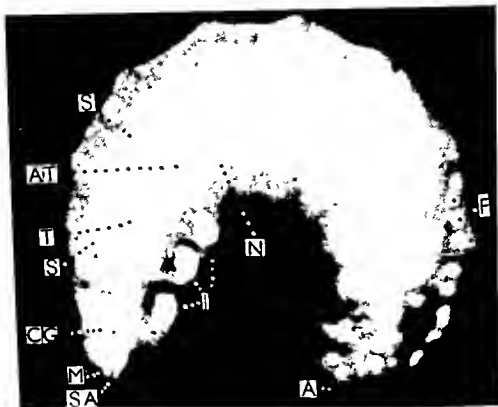


Fig. 219. Last instar larva of *Aphidius ervi* (photo courtesy of Dr. HOZÁK). M – mouth opening, CG – cerebral ganglia, A – anus, I – imaginal discs, N – nerve cord. S – silk gland, F – fat bodies, AT – alimentary tract, T – tracheae, SA – silk gland aperture, spiracles not recognizable on the picture.

free inside the body cavity of the host and this is why its spiracles come into active function.

Last instar larva may be considered the stage in parasite development, when the parasite becomes independent of the existence of the living host, but it is still unable to occur freely in the open; the last instar larva must, towards the end of its life, make certain modifications of the microenvironment of the aphid inside, as the following instars, before the adult parasite develops, are unable to develop a similar activity. Thus, the last instar larva mounts and constructs the cocoon, which must protect the prepupal and pupal stage from eventual injury. Contrary to the living parasitized aphid and the parasite adult, the prepupa and pupa are closed inside the cocoon and cannot find any shelters actively, thus they must be mounted to the surface as to a certain relatively fixed environment and the cocoon must protect them.

2. Cocoon spinning. After the larva has eaten all the content of the aphid and has killed it, it starts to spin the cocoon. First, before the true cocoon is spun, a small hole is cut at the ventral side of the aphid skin and the aphid is mounted to the surface by the secrete of the silk glands (Fig. 227). Then, the larva moves and turns inside the aphid skin, the silk glands being in action and the larva uses their excretion when constructing the cocoon. Movements of the larva inside the aphid skin are made

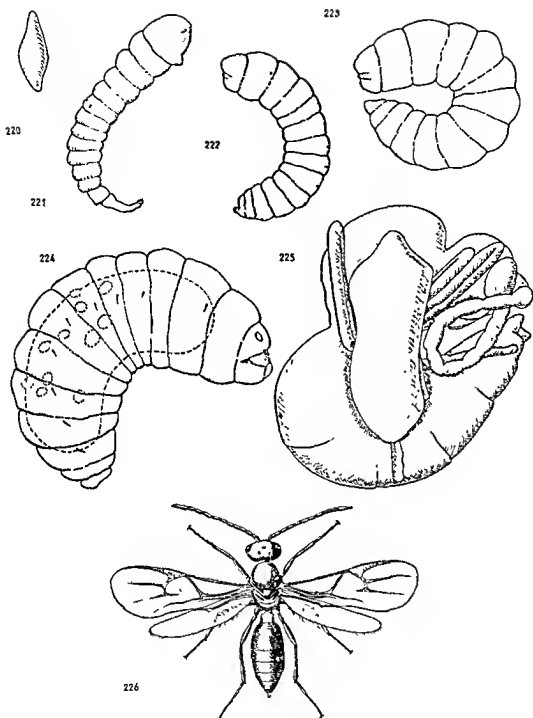


Fig. 220-226. Development of *Lysiphlebus fabarum*. 220. Egg. 221. Instar I larva. 222. Instar II larva. 223. Instar III larva. 224. Instar IV larva. 225. Pupa. 226. Adult female (all figures redrawn from TREMBLAY 1964).

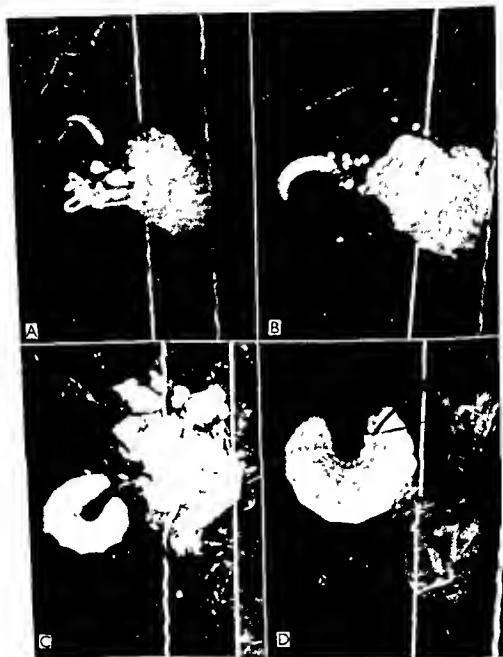


Fig. 227. Development of *Aphidius megourae*. A - instar I larva, B - instar II larva, C - instar III larva, D - instar IV larva.



Fig. 227. Development of *Aphidius megourae*. E - instar IV larva, killed host, F - instar IV larva, beginning of mummification, G - ditto, from beneath, H - ditto, mummification, movements of the larva.

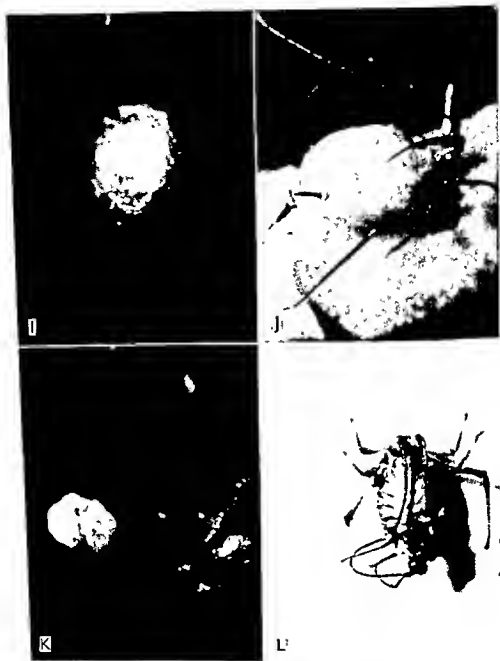


Fig. 227. Development of *Aphidius megoura*. I - mummified aphid from beneath, J - mummified aphid mounted on the surface of stem, K - pupa, taken out of the mummy, L - emerging adult parasite.

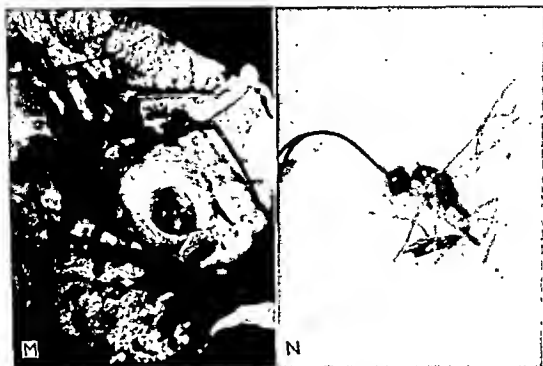


Fig. 227. Development of *Aphidius megourae*. M - empty mummified aphids after the parasite adult's emergence, N - adult parasite, ♀.

possible by the structure of its cuticle which bears small tubercles. The cocoon consists of several layers of silk, which are spun gradually on each other.

b. Mode of cocoon spinning. According to this the parasites are divided into the following groups:

The first group includes species where the larva spins the cocoon inside the skin of the parasitized aphid. This group is the most numerous (Figs. 227, 229-231).

The second group is characterized by the free separate cocoon, which the larva spins under the mummified aphid, the empty larval skin being situated at the top of the cocoon as a result (Fig. 232). This group is obviously derived from the original one mentioned above. We can recognize this easily from the comparison of the occurrence of both types among the aphidiids. While the first group is common, the second group includes only two genera, *Praon* and *Dyscritulus*, which are closely related to each other, *Praon* being more primitive. However, both genera are related to *Areopraon* and species of the latter genus spin their cocoons inside the parasitized aphid (Fig. 231). In *Praon* the cocoon is spun in a homogeneous way (Fig. 232), while in *Dyscritulus* a separate somewhat thicker margin can be distinguished, the rest of the cocoon being spun more feebly (Fig. 228).

The third group has recently been recognized by Dr. ZOULIAMIS (paper in preparation), who found a parasite (new genus?) of *Aphis fabae* in Greece to pupate in a different manner from the other parasites known. The last instar larva spins a separate, subglobular dark cocoon with a rough surface, while the aphid skin seems to be attached to any part of the cocoon whatever.

c. Appearance of mummified aphids. The spinning of a cocoon inside the host's skin influences the appearance of such a host considerably. The host skin becomes indurated, the segmentation is less distinguishable, if at all. The aphids are mounted

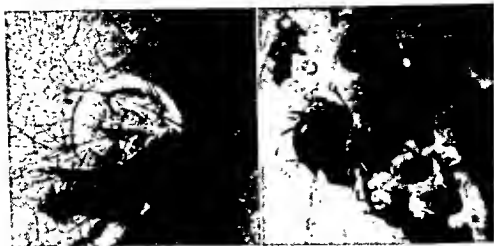


Fig. 228. *Drepanosiphum platanoides* on *Acer pseudoplatanus*. Cocoon of *Dyscritulus plantae* with alated aphid skin mounted on its top.

Fig. 229. *Aphis spiraephaga* on *Spiraea* sp., mummified by *Ephedrus plagiator*.

to the surface and their peculiar or "mummified" appearance as we call this makes them easily distinguishable in an aphid colony.

The aphids which are parasitized by *Praon* or *Dyscritulus* do not exhibit such features. This is obvious from the fact that they are not indurated but remain only empty as the cocoon is spun underneath the host skin.

d. Fixation of mummified aphids to the substrate. Before the larva spins the cocoon, it cuts a hole at the ventral portion of the aphid skin and mounts it to the substrate by the excretion of silk glands (Fig. 227). A small flat disc appears on the ventral surface of the parasitized aphid in consequence, which can be observed when the mummified aphid is carefully removed from the surface and put on its dorsum. When such a removal is made early in the cocoon spinning period, we can see through this semi-translucent disc the movements of the larva inside the aphid skin (Fig. 227). In some unusual cases, there is no fixation of the mummified aphid to the surface at all. This was observed in quiescent cocoons of *Ephedrus persicae* and *Monoctonia pistaciaecola*. In the former species, this could be due to the occurrence of the cocoons inside the leaf-curlings, in the latter species due to the occurrence inside the galls; both the environments obviously make the fixation of the quiescent cocoons unnecessary.

e. Coloration of mummified aphids. There are two aspects of the coloration of aphid mummies: we must distinguish the specific coloration and changes in coloration of the mummies due to their age.

The coloration of mummified aphids is specific. *Ephedrus* and *Pseudephedrus* (Figs. 229, 230) are responsible for a black coloration of mummified aphids, which is a generic character. Aphids mummified by most of the other aphidids are white yellowish to yellowish, brownish or dark brown to almost black. The cocoons of *Praon* species are whitish to yellowish or yellow brownish. Cocoons of *Dyscritulus* are translucent, with the external endurated portion whitish to yellowish (Fig. 228).

Using the differences in the coloration of mummified aphids, we can even sometimes recognize the parasite species which are represented in the colony: for example, in parasitized *Macrophegella*-species, the *Praon abnormis* cocoons are white-yellowish,

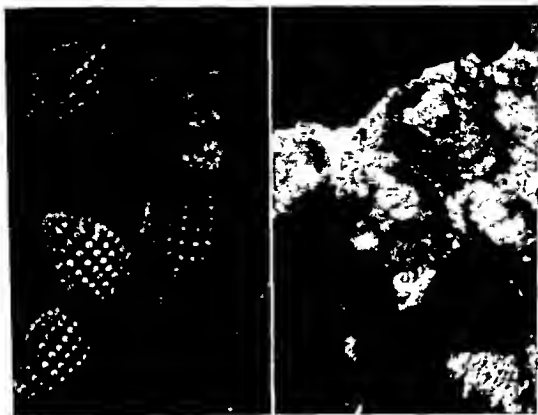


Fig. 230. *Neolizierius* sp. on *Nectandra reticularia*, mummified by *Pseudephedrus neotropicalis*.

Fig. 231. *Schizocura laugmosa* inside the gall on *Ulmus* sp. Aphids mummified by *Areopraon lepellei*, mummies with emergence holes.

with a separate cocoon beneath the aphid skin; the aphids mummified by *Ephedrus campestris* are black, those parasitized by *Aphidius absinthii* or *Trioxys centaureae* are brown to dark brownish.

Besides the peculiarities in cocoon coloration, we can observe the changes in coloration of mummified aphids in dependence on their age. The freshly mummified aphids, as soon as they become fully mummified, exhibit specific coloration. When they come of age, changes in their coloration are observed: the black mummies become black-greyish; the dark brown mummies become brownish; and the brownish or yellowish mummies reach almost entirely yellow-whitish to a whitish colour.

f. Surface of mummified aphids. The surface of a mummified aphid depends on the host aphid species which was mummified. However, due to the mummification of the aphid, especially if the cocoon spun inside is darker or black, the waxy covers of the aphid become more apparent. This phenomenon may be important when we have to distinguish mummified aphids belonging to several species that occur on the same plant and are similar when observed by the naked-eye in the field (e.g. *Hyalopteris pruni*, *Phorodon humuli*, *Myzus persicae*, *Brachycaudus cardui*, *Brachycaudus helichrysi*, etc., on *Prunus* species in spring in C. Europe).

Under certain circumstances the surface of mummified aphids may be secondarily changed. We omit such changes as the gradual break of legs, antennae, etc., of the aphid skin which are common, due to slight mechanical injuries, rain, etc. The typical secondary changes of a mummified aphid surface can be observed in *Prot-*



Fig. 232 *Eucreaphis punctipennis* on *Betula* sp.. Cocoons of *Praon flavinode* with aphid skins on their tops.

aphidius wissmannii: this parasite attacks and mummifies its host, the *Stomaphis*-species, in the usual manner. But the *Stomaphis* aphids are attended by *Lasius* ants and these ants exhibit somewhat unusual relations to the mummified aphids: they nibble the aphid skin and the true globular cocoon of the parasite remains free as a consequence of this action (see: ant-aphid-parasite relationship).

g. Non-quietescent and quietescent cocoons. Under certain circumstances, the larvae spin peculiar cocoons which differ from the normal cocoons. Quietescent states, especially obligatory diapause states, seem to be responsible for the induction of changes in the activity of the last instar larvae.

- PREPUA. The prepupa is a motionless state which lies passively inside the cocoon. There is, however, great activity inside the prepupa connected with the transformation of larval tissues.

- PUPA. The pupa is of the exarate type. A fresh pupa is whitish, gradually the separate body parts and regions become dark in accordance with the adult coloration. Eyes become pigmented first, being followed by the coloration of legs, antennae, head and thorax, while the abdomen bears the pupal character for the longest time.

From the ecological point of view, the pupal period may be considered as an intermediate state between the parasitic period of life and the period of free life of the adult: the pupa is still deposited inside or under the killed host, but there is no direct host influence on the pupa itself as the parasite pupa does not feed and exhibits its own respiration; however, the pupa is still influenced by the parasitized aphid in an indirect way as the living parasitized aphid is partially responsible for the transportation of the parasite larva inside its body. On the other hand, the external

environment may influence the pupa only through the cocoon or cocoon plus the host skin, inside which the pupa is situated (Fig. 227).

—ADULT. The parasite adult cuts a circular chink in the cocoon with its mandibles, presses out the central portion with its head and emerges. The central pressed-out portion forms the typical lid, which remains feebly attached to the margin of the emergence hole (Fig. 227). The larval skin and the meconium, which is represented by several dark corpuscles, remain inside the cocoon.

According to the position of the emergence hole, we divide the aphidiids into four groups.

Group 1. All the apical portion of the aphid is cut by the emerging parasite, a small cap remains hinged to the aphid skin. The apical portion includes the whole portion with the siphunculi, or the hole may be cut between them. Parasite genera: *Ephedrus*, *Pseudephedrus*, *Areopraon*, *Trioxys*, *Acanthocandus*.

Group 2. The whole apical portion of the aphid is cut by the emerging parasite, with a large cap remaining hinged to the aphid skin. This seems to be a similar mode of emergence as in group 1, however, the strongly spun cocoon seems to cause a somewhat different appearance of the apical cap. Parasite genera: *Protaphidius*, *Monoctonia*.

Group 3. Emergence hole is in the dorsal portion of the mummified aphid, somewhere between the thorax and the siphunculi. Usually, it is situated somewhat above the siphunculi. A circular hole is cut by the emerging adult parasite, the cut portion mostly or often remaining in a position forming a lid. This is the most common mode of emergence. Parasite genera: *Pauesia*, *Xenostigmus*, *Metaphidius*, *Diaeretus*, *Aphidius*, *Lysaphidius*, *Diaeretiella*, *Lysiphlebus*, *Lysiphlebia*, *Monoctonus*, *Paralipsis*, *Lipolexis*.

Group 4. Emergence hole is in the lateral portion of the parasite cocoon, the aphid skin being mounted at the top of the cocoon. A circular hole is cut by the emerging adult parasite, the cut portion mostly or often remaining in a position forming a lid. Parasite genera: *Praon*, *Dyscritulus*.

The shape of the emergence lid depends on the position of the emergence hole, and similar groups can be distinguished among the aphidiids. In the first group mentioned above, the lid has the shape of a small cap, which is mostly formed by the apical portion of the aphid or at least its part. In the second group, the lid is in the form of a larger cap, because of the construction of the cocoon. In the third group, which is the commonest, the lid is only slightly convex. The same is true as to the fourth group (Figs. 227, 230).

In the early post-emergence period the parasite adult spends a certain time in cleaning itself, moving its legs and antennae, the wings become adjusted. The content of the gut which is of a whitish colour, is excreted.

The adult stage is the only stage in the life of an aphidiid parasite that enables it a truly free life; during this developmental period, a parasite individual must find a favourable environment, a favourable host in this environment, find its mate or deposit progeny.

- REFERENCES. 3, 4, 21, 65, 98, 113, 129, 150, 153, 155, 158, 159, 211, 290, 298, 299, 300, 301, 343, 374, 417, 438, 460, 478, 483, 485, 500, 535, 536, 571-9, 588, 591, 597, 609, 642, 644, 646, 673, 679, 701, 681, 730-1, 762, 844, 890, 915, 917, 921, 985, 995, 1001, 1003, 1006, 1020, 1022, 1024, 1029, 1035, 1039, 1048, 1062, 1069, 1101, 1106, 1107, 1111, 1121, 1126, 1127, 1158, 1162-3, 1209, 1214, 1232, 1238, 1239, 1256, 1283, 1285, 1289, 1292, 1295, 1299, 1317, 1318-9.

Behaviour

- DIURNAL RHYTHM. The adult parasites are active during sunny warm days. They run along the plants, fly, and search for a mate, host and food. The greatest activity can be observed late in the morning and in the late afternoon. The hot noon and early afternoon hours are spent in less activity. In cloudy, rainy and colder days the parasites are little active, sometimes almost inactive, sitting motionless on the lower side of leaves. Sensitivity to conditions of relative humidity seems to be rather high. Adult parasites are inactive during the night.

Whether the movements along a plant are by running or flying depends on the species, e.g., the adults of *Praon abjectum* were observed to fly very often, while *Lysiphlebus fabarum* preferred running.

A period of warm sunny days following a longer period of cloudy colder days may cause an impression of a mass-flight of parasite adults (SKRIPTSHINSKIJ 1930); however, such a flight is due to the accumulation of parasites and inactive survival during the period of less favourable conditions.

- PHOTOTAXIS. Adult parasites, both ♂♂ and ♀♀, are positively phototropic. Naturally, their requirements as to light intensity are specific. Some species need open spaces with sufficient light, other species prefer semi-shaded undergrowth, some closed forest conditions, others occurring in forest ecotones, etc.

- BIOLOGICAL CONTROL. The knowledge of the diurnal rhythm of parasites is necessary in a parasite introduction program. The introduced parasites must be released on suitable days and on a suitable period of days in the new environments. Consequently, release of parasites is generally recommended to be undertaken during the morning hours or late in the afternoon, on bright, sunny and warm days.

Positive phototropism of parasite adults may be successfully used in laboratory mass-rearings, where the emerged parasites can be collected on the upper side of rearing cages near to the light. Various adaptations in rearing rooms may be developed on this base.

REFERENCES. 65, 417, 459, 642, 679, 681, 762, 1003, 1005, 1022, 1062, 1101, 1125, 1158, 1162, 1266, 1309.

Longevity of Adults

General records on parasite adult longevity can be found in a number of different papers (ARTIUR, 1944—*Aphidius avenae*, BODENHEIMER & NEUMARK, 1955—*Pauesia* sp., GRIOT 1944—*Lysaphidus platensis*, MILLAN 1956—*Lysaphidus platensis* SEDLAG 1964—*Diaeretiella rapae*, SKRIPTSHINSKIJ, 1930—*Aphidius avenae*, *Ephedrus plagiator*, TREMBLAY, 1964—*Lysiphlebus fabarum*, etc.). Such data, however, are too generalized to be of use for detailed ecological studies. Such studies, as those undertaken by BROUSSAL (1966), SCHLINGER & HALL (1960, 1961), FORCE & MESSENGER (1964), WIACKOWSKI (1962), etc. clearly documented the significance of the research of the requirements of parasite adults on environment. They have shown that longevity of adults, a specific phenomenon, is influenced by a number of various factors, and, simultaneously, represents an important feature of parasite biology.

- FACTORS. 1. Temperature is the main factor influencing adult longevity. Both low or too high temperatures influence it considerably (WIACKOWSKI, 1962) as well as oviposition, mating activities, etc. Detailed experiments of FORCE & MESSENGER

(1964) made on *Praon exoletum* and *Trioxys complanatus* showed that there was little difference in mean longevity between 18.3°C and 21.1°C, although a small percentage survived for a longer period at a cooler temperature. Similarly, there was little difference between the overall survival time at 23.9°C and 26.7°C. However, a large difference between 21.1°C and 23.9°C suggests that some temperatures within this range greatly affect the physiology of the insect with respect to its longevity. As to natural conditions, it is necessary to stress that temperature conditions fluctuate. Temporary unfavourable conditions can deeply influence the parasite adults, as observed by LUZHETSKI (1960) in Asia, where temperature over +30°C caused mass-decline of *Lysiphlebus fabarum* adults.

2. Relative humidity is rather important too. In experiments by WIACKOWSKI (1962) using *Aphidius smithi* in connection with honey as food R.H. had an increased effect, with the exception of low (1.7°C) and high (32.2°C) temperatures.

3. Photoperiod. Although we have no experimental records at hand, it is probable that the photoperiod influences adult longevity as well, as the adult parasites are generally inactive at night, while their activity is apparently influenced by the length of the light period. Certain observations of this kind were carried out by BROUSSAL (1966) but the influence of photoperiod in this case could be obscured by the intrinsic differences between hibernating and aestival parasite generation, temperature and R.H. influence, etc.

4. Season. Two points of view exist on the relation of season and adult longevity.

First, there are differences in adult longevity in various seasons of the year due to different climatic conditions. In a temperate zone, the longevity of adults is longer in spring and in autumn as the temperature is relatively lower, while it is short during a hot summer. HAFEZ (1961) found that in the Netherlands in early spring the mean longevity of *Diaeretiella rapae* was about two weeks, while it gradually decreased to one week under mid-summer conditions.

However, BROUSSAL (1966) found that differentiation exists between various generations of *D. rapae* in France, when they are reared under the same conditions in the laboratory: when reared under an 11 hour period, 20°C and 80% R.H., the early spring generation longevity was 10 days for virgin ♀♀ and 11 days for mated ♀♀, while it was 11 days for virgin ♀♀ and 13 days for mated ♀♀ in the aestival generation. Apparently, the conditions under which the parasites must survive (hard winter, etc.) cause these differences.

5. Various kinds of food are sometimes the cause of the prolongation of adult parasite longevity to a various degree. Some kinds of food are disregarded, others are accepted but longevity is only somewhat longer, others still are accepted and prolong the longevity in a rather significant way (see: Food of adults).

Honey, a suitable laboratory food of parasite adults, was tested with respect to *Aphidius smithi* longevity in the laboratory by WIACKOWSKI (1961): with probably the exception of 1.7°C when honey was probably not ingested, at all the other temperatures the honey supply brought about a marked increase in the longevity of adults: 10.0°C—2.1 times, 15.6°C—5.8 times, 21.1°C—4.8 times, 26.7°C—4.8 times, 32.2°C—1.5 times.

6. Sex. Apparent differences in adult longevity in various temperatures with respect to sex have been recognized by various authors. SCHLINGER & HALL (1960) found that ♂♂ of *Praon exoletum* showed generally greater longevity than the ♀♀, however, under certain temperatures there were almost no differences (Fig. 233). WIACKOWSKI (1962) recognized differences in ♂ and ♀ longevity in all the temperatures studied, the ♀♀ living generally longer than ♂♂. On the contrary, HAFEZ (1961) found no differences in longevity of ♂♂ and ♀♀ in *Diaeretiella rapae*. H : 20

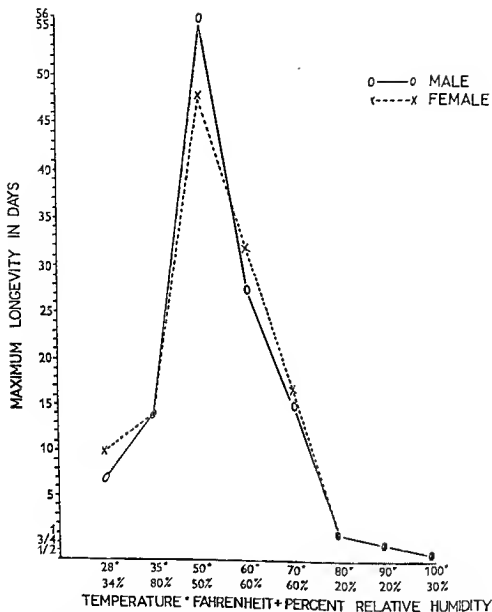


Fig. 233. Longevity of adults of *Praon exoletum* (= *palitans*) under various combinations of constant temperature and relative humidity and with honey as food source (SCHLINGER & HALL 1960).

ever, were obtained under fluctuating temperatures in the field and need experimental proof under constant temperature conditions as well.

7. Host gives the parasite ♀ a possibility to oviposit and consequently decreases their supply of energy. WIACKOWSKI (1962) ascertained that ♀♀ of *Aphidius smithi* lived the shortest time in the presence of live aphids as the presence of aphids and their movements stimulated the ♀♀ to lay eggs and to increase the activity: longer longevity of ♀♀ was found in the absence of the host, while ♂♂ did not show such differences.

8. Mating has a significant influence on adult longevity. This influence, however, is different in ♀♀ and in ♂♂. BROUSSAL (1966) found that irrespective of generation mated ♀♀ showed greater longevity than virgin ♀♀; (see p. 59)

Although we have no detailed observations as to the influence of mating on ♂ longevity, it is probable that mating in ♂♂, due to the searching activity and copulation, will manifest a similar effect on the adult longevity as oviposition in the case of ♀♀. Consequently, ♂♂ will apparently live longer in the absence of ♀♀. Indications of such differences were mentioned by V.D. BOSCH et al. (1966) in *Aphidius smithi* in California, where ♂♂ prevailed in wasps that accumulated during cool weather on the mid winter alfalfa crops.

The above mentioned factors are complex in action. However, we can distinguish various degrees of importance among them. Temperature and R.H. have a dominant role, while food seems to be a third one. Two examples may be mentioned to show, at least partially, the interrelations of factors mentioned above: Tests on the longevity of *Praon exoletum* and *Trioxys complanatus* in dependence on temperature, R. H. and food, undertaken by SCHLENGER & HALL (1960), showed that both with and without honey, the longevity curve was about the same, but values were higher in the presence of food.

Similarly, as ascertained by WIACKOWSKI (1962) in *Aphidius smithi*, with the exception of extremely low (1.7°C) and high (32.2°C) temperatures, the higher the degree of R.H., the greater was the effect of food.

— SIGNIFICANCE. The adult stage is the only free stage of the parasite during the development. Consequently, a great number of activities must be undertaken by the adults as the other stages are unable to do so: mating, reproduction, host finding, etc., are the obvious examples.

Longevity represents one of the responses of the adults to environmental conditions. During their lifetime, adults must principally mate and find hosts in order to secure population existence in a given plot. Low temperature conditions prolong the life of adults, but they simultaneously correspondingly reduce the activity of adults; high temperatures, on the contrary, stimulate parasite adult activity, but the lifetime is shorter, the optimum lifetime seems to be one where the adults may realize all their biological needs in the most suitable manner. The optimum is relative in nature as a species must adapt itself to environment. Adults occur during a part of the season under optimum conditions, but generally the conditions fluctuate both during a day or a part of the season, and, consequently, corresponding differences are found in the biological activities of the adults.

— BIOLOGICAL CONTROL. 1. Survival. Various species of parasites show different requirements on temperature conditions in an adult stage. These requirements also determine their microhabitat distribution. On the base of knowledge of temperature requirements of separate species, we can recognize the laws of their distribution in the release area and their probable further distribution. Such a difference between introduced species was established in parasites of *Therioaphis trifolii* in California, *Trioxys complanatus*, which preferred microhabitats with higher temperature conditions, while *Praon exoletum* occurred in microhabitats where temperature was generally lower (see: V.D. BOSCH et al., 1964, FORCE & MESSENGER, 1964).

2. Seasonal changes. Observations have shown that there may be differences in longevity of various generations during the year. In addition, changing temperatures during the yearly seasons also influence adult longevity. Through the longevity the temperature conditions influence searching ability, oviposition and mating activities, dispersal, etc., of the species.

3. In the mass-rearing of parasites, the knowledge of the responses of adult para-

sites to the influence of various temperatures, R. H. and food enables us to control these conditions in the most suitable manner. This was practically demonstrated by FORCE & MESSENGER (1964) and other Californian authors.

4. Storage of adult parasites is an important part of a parasite release program. As usually not such a number of parasites that has to be released can be produced in an insectary, the parasite adults are stored for a certain time. For example, STARÝ (1964) showed that the adults of *Aphidius megourae* survived temperatures up to below 0°C while -5°C were lethal. Experiments also showed that in a changing temperature of +5°C to -5°C the adults, having been kept at +10°C later and then at +18-24°C can attack the aphids in about 15 minutes. The ♀♀ used in experiments attacked aphids and laid eggs in +18-24°C after having spent 14 days in +5 to -5°C, 20 eggs were laid and the progeny was normal, including both ♂♂ and ♀♀.

Evidently, in this parasite, both eggs and sperm, also in the ♀ spermatheca, can survive temperatures up to -5°C for at least a fortnight. However, as observations have shown (WIACKOWSKI, 1962 in *Aphidius smithi*), a too long cold storage can be detrimental as to the quality of sexual products of parasite adults.

5. Although shipping methods are mostly well elaborated, it is generally recommended to ship the parasite adults in such a period of the year when the temperature conditions are neither too cold nor hot and thus would not negatively influence the shipped material.

REFERENCES. 21, 98, 128, 130, 158, 417, 482, 497, 655, 679, 762, 1003, 1005, 1020, 1022, 1062, 1111, 1121, 1125, 1127, 1158, 1231, 1295, 1299.

Food of Adults

The aphidids are parasitic during their development in aphids, their adults being free-living insects. This difference in the mode of life, which is just typical for all the parasitoids, is connected with different food requirements as well. The free life of adults is conditioned by other food sources than those of their larvae—the host body fluids. Although the adults may live for a certain time without food, food is necessary for their further occurrence.

- *Water* is necessary for adult parasites after several hours of their post-emergence life. After they have emerged the adults may mate and also oviposit in case of mate or host presence, but they soon stop these activities and can be observed running nervously in search of water. Without water, they die rather soon after emergence, while a water supply enables them to survive for a minimum period, which can be prolonged by feeding on a suitable kind of food. Water and honeydew seem to be the main sources of food of parasite adults in nature.

- *Honeydew of aphids.* According to the qualitative analysis of honeydew by AUCLAIR (1963) it consists of carbohydrate constituents, nitrogenous constituents, and miscellaneous compounds. As to the carbohydrates, fructose, glucose and sucrose are the main kinds represented. Therefore, honeydew is a source both of carbohydrates and proteins. The aphidid adults, when feeding on honeydew, satisfy both their carbohydrate and probably also protein needs and, consequently, they do not need to feed on their host through mutilation. This is contrary to the opinion of MILLAN (1956) who derived from the absence of host mutilation in the aphidids that they do not need proteins during their adult life.

- *Fresh and dry honeydew.* - Observations of various authors as well as our own observations have shown that there are obvious differences between fresh and dry



Fig. 234. *Aphidius ervi* adult feeding on honey.

honeydew as food for parasite adults. SPENCER (1926) was perhaps the first who recognized that the parasites do not "milk" the aphids and eat the honeydew direct from them as some insects are reported to do, but lap it from the top of the lower leaves which often become varnished with the honeydew material dropped from above. We have observed that dry honeydew exclusively was fed on by parasite adults, while fresh honeydew was omitted (Fig. 234). LEIUS (1960) found that honeydew is an important source of food and moisture for ichneumonid parasite adults especially in early spring and late autumn when flowering plants are scarce; however, in hot sunny summer days the adults abstained from honeydew, possibly due to early fermentation and quick drying of honeydew. It is obvious from the comparison of these facts that the adults of some parasitic groups prefer fresh honeydew, the other groups preferring it to be dry. To the later group the aphidius belong. Apparently, the consistency of honeydew is not significant as the aphidius feed also on droplets of a honey or sugar solution, but the fermentative changes in dry honeydew are perhaps most important.

A special kind of honeydew as food of parasite adults seems to be honeydew milked by ants and later supplied through regurgitation to *Paralipsis enervis* adults as the consistency of this honeydew is liquid.

- Feeding on honeydew - The observations of various authors have proved satisfactorily that the honeydew of aphids is the main source of food of parasite adults: SPENCER (1926)—various species, ARTHUR (1944)—*Aphidius avenae*, GYÖRFI (1945)—various species, MILLAN (1956)—*Lysaphidius platensis*, SEKHAR (1957)—*Lysiphlebus testaceipes* and *Praon aguti*, SCHLINGER & HALL (1960)—*Praon exoletum*, SCHLINGER & HALL (1961)—*Trioxys complanatus*, SEDLAG (1964)—*Diaretella rapae*, etc. We have observed adults of many species (*Aphidius ervi*, *Lysiphlebus fabarum*, etc.) feed on the dry honeydew of their hosts in the laboratory.

hosts is necessary to obtain the protein needed for oogenesis (DOUTT, 1964). This predation may be obligatory or facultative (FLANDERS, 1953). Among the parasites of aphids a similar behaviour is known to occur in certain aphelinids, whose ♀♀ puncture the host aphid for nourishment and then they feed on the body fluids (WILBERT, 1965).

A similar predatism is unknown among the aphidiids. Although aphidiid ♀♀ may often be observed to insert the ovipositor and not to lay eggs, this behaviour is due to factors influencing oviposition and is not connected with feeding on the host. As mentioned correctly by DOUTT (1964), the protein requirements in species that do not feed on their hosts may be supplied by feeding on honeydew or on plant nectaries, both of which have been shown to contain free amino-acids. The above mentioned is supported by WIACKOWSKI (1962) in observations made on *Aphidius smithi*, where the ♀ parasites did not feed on dissected *Acyrtosiphon pisum* either. We have obtained the same results in *Aphidius ervi* (STARÝ 1962).

—Honey. Honey and water were found to represent the most suitable food of parasite adults in the laboratory. This kind of food was successfully applied by SKRIPTSHINSKIY (1930)—*Ephedrus plagiator*, *Aphidius avenae*, SCHLINGER & HALL (1960)—*Praon exoletum*, SCHLINGER & HALL (1961)—*Trioxys complanatus*, HAFEZ (1961)—*Diaretella rapae*, STARÝ (1962)—*Aphidius ervi*, WIACKOWSKI (1964)—*A. smithi*, etc. STARÝ (1964)—*A. megourae*, etc.

According to our observations honey and water seem to be a kind of laboratory food applicable to all parasite species reared in the laboratory (*Aphidius megourae*, *Praon abjectum*, *Trioxys angelicae*, *Ephedrus plagiator*, *Lipolexis gracilis*, *Lysiphlebus faharum*, *Aphidius ervi*, etc.).

—Syrup. Syrup as a laboratory food of *Diaretella rapae* adults was used by BROUSSAL (1964).

—Agar and other laboratory foods. Various mixtures were used as food by various authors. Solutions of various carbohydrates are the most common: SUBBA RAO & SHARMA (1962) used 10% sucrose solution as laboratory food of *Trioxys indicus* adults. SEDLAG (1964) used a sugar solution for *Diaretella rapae*.

According to the observations of STARÝ (1964) a glucose solution prolongs the parasite adult life to a certain degree, it was not, however, too suitable if compared with honey; on the contrary, dried glucose was apparently ignored by *Aphidius megourae* adults as their longevity was identical as if only water was present. The ignoring of dried glucose was also observed in *A. ervi* adults (STARÝ, 1962). However, glucose and water combinations were found more suitable than honey by this parasite.

Observations of SEKHAR (1957) gave negative results as to the sugar solution as laboratory food of *Lysiphlebus testaceipes* and *Praon aguti* adults.

Agar and different proportions of sugar and honey as laboratory foods were used by various authors (HAGEN 1964, MILLAN 1956).

STARÝ (1962) tried dried yeasts as a laboratory food of *Aphidius ervi* as a possible source of protein. The results were negative.

—SEARCHING FOR FOOD BY ADULTS. The food searching behaviour of parasite adults does not seem to be well differentiated from searching for host of the ♀ or searching for the ♀ by ♂ parasites. According to SCHLINGER & HALL (1961) ♀ *Trioxys complanatus* were observed to walk with their heads down and palpi in contact with the leaf surface; consequently, the palpi are thought to be used in locating the honeydew. This observation seems to be correct. We have also observed adults to palpate drops of honey before feeding on them (Fig. 234). However, in the presence of hosts and lack of water and adult food the parasites are observed to stop oviposition and search in

the neighbourhood; their behaviour is identical as in the search for hosts or mates (antennal tapping), but they leave the hosts untouched in the case of tapping it. Thus we can suppose that the adults are searching for food. It seems that water or food is primarily searched for through the antennal tapping and consequent stimuli come through the sensory organs located on the antennae; the detailed search for adult food is realized through palpating the food.

— **FOOD OF ADULTS WITH RESPECT TO SEX.** Food requirements seem to be identical in both ♀♀ and ♂♂. In both sexes, stimuli due to the lack of food are apparently of secondary significance in the early post-emergence life: ♀♀ may oviposit and mate, ♂♂ may search for ♀♀ and mate without feeding. However, this is true only of post-emergence, as the adults soon interrupt oviposition, mate-searching, etc., and search intensively for water and food. Their post-emergent state is apparently possible due to the supply of water and food present in their bodies early after emergence.

— **FACTORS AFFECTING FOOD ACCEPTANCE.** Food acceptance may be influenced possibly by two factors which are overruling it in action:

Low temperature may result in a greater or lower activity of adults which, consequently, feed very little. High temperatures may change the consistence of food (honey), so that it is not ingested (WIACKOWSKI, 1962).

Investigations of the interaction of food and R.H. showed (with exception of temperature 35° and 90°F) that the higher the degree of R.H., the greater the effect of food (WIACKOWSKI, 1962, *Aphidius smithi*).

— **SIGNIFICANCE.** Adult parasites can survive considerably long periods under various temperature conditions in case of the absence of mate or host. Although the minimum period of occurrence is due to the supply of energy from the pupal period, at least water is necessary if longer periods have to be survived.

— **Longevity.** Food is one of the basic factors determining the longevity of parasite adults (see below). Although temperature is the most significant factor, the presence or absence of food is responsible for the relative difference in values.

— **Fecundity.** The presence of food is one of the factors influencing the parasite reproductive capacity through longevity and supply of energy.

— **Oviposition.** A ♀ can oviposit for a certain period after emergence, but water and food is necessary in the case that oviposition is to be continued for a longer period. However, it is not clear yet whether food is accepted as a source of energy or whether it is of direct importance for egg production.

— **Mating.** Newly emerged adults can mate without accepting food. But multiple matings in ♂♂ are apparently conditioned by the presence of food sources.

— **Attractant.** Honeydew as a source of food of adults may also play a role of an attractant of the parasites to an aphid colony.

— **BIOLOGICAL CONTROL.** It is known that adult food of a number of insect parasites is searched for by parasite adults at other places than on the place of the occurrence of the host. The distribution of such groups often depends on the presence of a dult food—in case of its absence the parasite is unable to occur in the place even if host were present. The attachment of various ichneumonid groups to flowering plants can serve as an example.

Contrary to the parasite groups mentioned above the aphidius feed on the honeydew of their hosts and they do not require special sources of food such as flowering plants, etc. Their occurrence and that of their hosts is identical in this respect.

— **Secondary importance of food stimuli.** Parasite adults are able to oviposit and mate without feeding on water and honeydew in a certain period of their early post-emergence life. This is a rather important phenomenon as it enables the parasite to produce a part of its progeny in the given host-population and to secure survival in

the given area even in absence of food; however, the source of adult food is conditioned by the occurrence of the host.

— *Other entomophagous insects.* Honeydew is not the food of aphid parasite adults only. Many other parasitic and predatory insects feed on it as well. ZOEBELEIN (1956), listed 246 honeydew feeding insects, including obligatory feeders such as ants, or facultative feeders such as adults of tachin flies, ichneumonid flies, braconids, syrphids, coccinellids, etc. Consequently, honeydew is an important source of food of quite a number of useful insects, not to speak of its significance in apiculture. Economically indifferent aphid species namely might be important in this respect, representing either alternative hosts of aphid parasites, or indirect sources of food of the adults of aphid and other parasites and predators.

— *Laboratory foods.* As the food influences the longevity, oviposition, etc., it has a great significance in mass-rearings of the parasites. Various media were used in experiments, but it seems that honey and water are the best of them. Although they represent a food that cannot be obtained by parasite adults in nature, honey is widely used in the mass-rearing of various parasite species. This feature of parasite biology can be used in various experimental studies where the absence of host is required. In shipping techniques, too, where simultaneous shipping of the host is mostly excluded due to its rather short longevity and difficulties connected with the growing of plants, the parasites are sometimes shipped as adults or they may emerge from the shipped mummified aphids during transport; the presence of suitable laboratory food enables their survival for a considerable period, and consequently, better results are obtained as to the number of living specimens shipped.

REFERENCES. 21, 26, 51, 65, 155, 222, 290, 294, 355, 390, 400, 421, 453, 474, 492-3, 497, 499, 505, 546, 548, 643, 654-6, 719, 735-6, 762, 774, 1003, 1005, 1022, 1023, 1062, 1101, 1111, 1121, 1158, 1222, 1299, 1304, 1338-40.

Mating

The aphidiids include mostly biparental species. For this reason mating is a normal and necessary part of the life-cycle of each parasite species.

Swarming as a mating habit is known to occur in many insects, in braconid wasps as well (*Blacus* species). STELFOX (1957) described a mass-flight of *Ephedrus validus* from Ireland. Mass-occurrence of *Lysiphlebus testaceipes* was mentioned by WEBSTER & PHILLIPS (1912) and others. However, it must be stressed that there is a basic difference between swarming and mass-flight. Swarming is characterized by mass-occurrence and typical swarming flight and is a typical behavioural pattern. Such a pattern was not observed among the aphidiids. The mass-flight of aphid parasites is not a behavioural feature, but it is a consequence of high density of host aphids and a high percentage of parasitization. Naturally, mass-flight of emerging parasite adults provides better conditions for both sexes to meet.

— *PREMATING PERIOD.* The interval between the emergence and mating—the pre-mating period—is of various length in the aphidiids. In most species, mating may take place almost immediately or soon after emergence: *Aphidius avenae*: SKRIPTSHINSKIJ, (1930), MACGILL (1923); *A. smithi*: WIACKOWSKI (1962); *Diaeretiella rapae*: HAFEZ (1961); *Lysiphlebus fabarum*: LUZHETSKI (1960); *Pauesia* sp.: BOENHEIMER & NEUMARK (1955); *Praon exoletum*: SCHLINGER & HALL (1960); *Trioxys complanatus*: SCHLINGER & HALL (1961); *Tr. indicus* (1962), etc.

In *Aphidius smithi*, the pre-mating period under 25°C lasted 3.5 min. depending on air temperature and activity of ♂♂ (WIACKOWSKI, 1962).

Other species require a longer time before being able to mate after their emergence. SEKHAR (1957) experimentally ascertained on the basis of 3 hours observation made on parasites, that of 50 pairs of *Praon aguti* no mating occurred within the first hour and a half of observation, but more than 20% of the pairs mated within the next half hour (25-35°C, 75-86% R.H.).

— MATING BEHAVIOUR. 1. Virgin female behaviour. A virgin ♀ is entirely passive as to the mating activity until it is found by the ♂. As oviposition may take place without mating it seems the searching for the host and oviposition are the main and prevailing stimuli acting in a ♀'s behaviour, while mating behaviour must be stimulated by the presence and activity of a ♂. Virgin ♀♀ apparently produce a certain characteristic odour that causes them to be found by the ♂♂.

2. Searching behaviour of male. A ♂ searches for a ♀ by running and flying. The prevalence of running or flying is specifically dependent. A ♂ detects the presence of a virgin ♀ by odour. Experiments undertaken by several authors represent a satisfactory proof. SUBBA RAO & SHARMA (1962): *Trioxys indicus*, SCHLINGER & HALL (1960): *Praon exoletum*. ♂♂ were found to detect the ♀ presence apparently by odour, however, in no case was the ♂ able to detect the virgin ♀ while she was in her cocoon, even just prior to her emergence.

3. Act of copulation. As soon as the ♂ comes in the presence of a ♀ and sensory contact is made, he exhibits great excitement which can be recognized from his running around, movements of antennae and characteristic vibration of wings. Antennal tapping is then usually exchanged between the ♂ and ♀. Attempts of the ♂ to mount the ♀ follow. At this stage the ♀ sits quietly with her wings on her back, while the ♂ vibrates his wings rapidly and taps the ♀ quickly with his antennae. This behaviour continues unchanged during the copulation act, which is started by the ♂ in bending the hind region of the abdomen downward and meeting the sex organs of the ♀. Copulation is mostly terminated by the ♀. In case the ♀ moves away before the ♂ was able to mount her, he follows her, tapping her by his antennae and trying to mount her. The length of the copulation act is different in separate species:

Aphidius ervi: about 40 sec., STARÝ (1962); *Aphidius smithi*: 15-80 sec., WIACKOWSKI (1962), etc. It is necessary to stress that to be successful the copulation act must last a minimum time, otherwise the copulation is unsuccessful and the ♀ produces unfertilized eggs exclusively. WIACKOWSKI (1962) gives 15-80 sec. to be the range of the lasting of the copulation act; however, 15-25 sec. were ascertained to be unsatisfactory for a successful copulation. It is probable that a similar situation occurs in other parasite species too.

4. Post-copulation behaviour. After the copulation act is completed the ♀ usually remains quiet for some time, or it cleans itself or runs a little.

While the ♂ exhibits the same type of mating behaviour to other virgin ♀♀, the mated ♀ basically changes its behaviour and refuses to be mated for the second time by a ♂ (see below). Oviposition may or may not follow after mating is finished, the presence of a suitable host being a necessary condition.

— FACTORS. 1. Synchronization of emergence of males and females. There is apparently no synchronization in the emergence of ♀♀ and ♂♂ in the aphidids. This feature seems to be due to the effect of factors that influence the oviposition of ♀♀. As a result, both sexes emerge independently of each other as to time.

2. Virgin or mated female. A once mated ♀ apparently loses its characteristic odour and it simultaneously changes its behaviour. Under certain conditions, the copulation act may be incomplete, or a young virgin ♀ may be mated by an old ♂ whose

supply of sperm is very low. However, the ♀ cannot be mated more successfully for the second time and male progeny is consequently produced due to the lack or low supply of sperm in the ♀'s spermatheca.

3. Oviposition. According to the observations of VEVAI (1942) on *Aphidius matricariae*, and of SUBBA RAO & SHARMA (1962) on *Trioxys indicus*, ♂♂ are unsuccessful in mating virgin ♀♀ which had already commenced ovipositing parthenogenetically, the ♀♀ actively resisted the attempts of the ♂♂ to copulate, as did mated ♀♀. This means that oviposition which occurs earlier than mating prevents the mating of a virgin ♀ if the ♂♂ later appear.

Unfortunately, there is lack of information on this feature in other aphidiids. If it would be a general feature of parasite biology, its importance would be obvious with respect to the relation of host and parasite densities, searching abilities of ♀♀ and ♂♂, etc.

4. Searching ability of males. As mentioned above, no mating is possible in certain species if oviposition precedes mating. The searching ability of ♂♂ is therefore important. The ♂♂ must search for the ♀♀ quickly to find them before they begin ovipositing.

5. Number of matings in males. The gradually higher number of matings causes the simultaneous exhaustion of the ♂ and this results in a lower quality of mating (see below).

6. Length of the copulation act. Various stimuli may cause an early break of the copulation act. Consequently, mating may be classified as incomplete. For example, WIACKOWSKI (1962) observed mating in *Aphidius smithi* to be completed in 15-80 sec., but when copulation was limited to 15-25 sec., only ♂ progeny was produced; probably the period was too short to transfer the sperm to the ♀'s reproductive system.

7. Temperature. Both too high and too low temperatures may prevent the mating. Temperature at or above 35°C caused adults of *Lysiphlebus testaceipes* or *Praon aguti* to fly restlessly about and no mating took place, a decrease of temperature brought about an increase in the number of matings (SEKHAR, 1957).

It may be generally observed in nature that in sunny and warm days the parasites are rather active, both as to mating and searching for the hosts, while adverse weather conditions cause a decrease of their activity.

8. Age of female and male. It seems that generally the most favourable time for mating is the first 24 hours after emergence. Later, the sexual instinct seems to be gradually lower. WIACKOWSKI (1962) found that it is only rarely that the ♀ *Aphidius smithi* would mate two days after emergence, while copulation was never observed on the third day after emergence, despite the great activity of the ♂♂. According to VEVAI (1942) the sexual instinct is lost earlier in the ♀♀ than in the ♂♂ in *A. matricariae*.

The age of the ♂, although it may copulate during its lifetime, conditions the length of the copulation act and the interval between the matings (SCHLINGER & HALL, 1960, 1961).

9. Food. SEDLAG (1964) ascertained that mating is possible also in case of lack of preceding feeding. The presence of food, however, appears to be essential to multiple matings (WIACKOWSKI, 1962).

10. Sex ratio. A too low number of ♂♂ and high proportion of ♀♀ apparently cause the occurrence of many unmated ♀♀ in a given plot.

11. Population density. Low density of host population forces the ♀♀ to search for hosts for a longer time and this gives the ♂ a better chance to find the ♀ before it commences to oviposit. On the contrary, a high host density enables the ♀ to start ovipositing prior to being mated.

12. Photoperiod. As is apparent from our numerous reared samples taken in the

field, the mated ♀♀ in biparental species can be found throughout the whole season. Detailed observations were made by BROUSSAL (1966), who found mated and virgin ♀♀ to occur both in early spring and aestival generations of *Diaeretiella rapae* in France. The photoperiod, therefore, does not seem to significantly influence the mating.

—NUMBER OF MATINGS IN FEMALES. Numerous observations of various authors agree in that there is only a single mating in ♀♀ during their lifetime: SEKHAR (1957)—*Praon aguti*; WIACKOWSKI (1962)—*Aphidius smithii*; STARÝ (1962)—*A. ervi*; STARÝ (1964)—*A. megourae*; SCHLINGER & HALL (1960)—*Praon exoletum*; SCHLINGER & HALL (1961)—*Trioxys complanatus*, etc.

FLANDERS (1946) separated the parasite ♀♀ into two groups in dependence on the number of matings: multinuptial species mate several times during their life, while uninuptial species mate only once in their life. Because of the features of the biology of the aphidiid wasps, all the biparental species of aphidiids must be classified as belonging to the uninuptial group.

—NUMBER OF MATINGS IN MALE. MULTIPLE MATINGS. Contrary to ♀♀, multiple matings seem to be normal in ♂♂. The matings may take place during one or several days.

Various authors mentioned the number of multiple matings in different species as follows:

Aphidius matricariae: 13–18, VÉVAI (1942); *Lysiphlebus testaceipes*: 19, SEKHAR (1957), etc. The number of matings is apparently conditioned by the presence of food (WIACKOWSKI, 1962) and by temperature conditions (TREMBLAY, 1964).

—INFLUENCE OF MATING ON FEMALE. 1. Odour. Mating apparently causes the loss of odour which is typical of virgin ♀♀. This loss of odour prevents the mated ♀ from being detected by ♂♂ unless they accidentally come into physical contact with her (SCHLINGER & HALL, 1960, *Praon exoletum*; SCHLINGER & HALL 1961, *Trioxys complanatus*). Besides the active repelling of ♂♂, mentioned below, this loss of odour seems to be a passive adaptation of a mated ♀ to prevent further mating.

2. The behaviour of ♀♀ changes markedly in dependence on mating. This feature may be commonly observed in all the aphidiid species and has been mentioned by various authors.

A virgin ♀ does not resist the attempts of a ♂ to copulate, corresponding behaviour being observable. This behaviour of the ♀ strictly changes after it is mated as it actively repels a ♂. SCHLINGER & HALL (1960, 1961) made detailed observations on this changed behaviour due to mating: in *Trioxys complanatus*, when ♂♂ were placed with recently mated ♀♀, they were always discouraged from mating. The ♀ either ran away or bent its abdomen under so that copulation could not take place; a rather common act of discouragement on the part of the ♀ was one of striking at the ♂ with the ovipositor. Similarly, in *Praon exoletum*, the ♂♂ being placed with recently mated ♀♀, when the ♂ attempted to copulate, the ♀ inevitably discouraged him by moving away, or by pushing him off her back with her hind legs; if the ♂ persisted, the ♀ would bend her abdomen down, thus preventing copulation.

3. Longevity. According to observations of BROUSSAL (1966) made on *Diaeretiella rapae*, mated ♀♀ exhibited greater longevity than virgin ♀♀, irrespective of whether they belonged to spring or aestival generations.

4. Oviposition. Observations of various authors have shown that the ♀ oviposits irrespective of whether they were mated or not. Oviposition stimuli seem therefore to overrule the mating stimuli.

5. Mating means the presence of a larger or smaller supply of sperm in the ♀ spermatheca. Consequently, by regulation of this sperm supply, the ♀ may determine the sex of its progeny.

- INFLUENCE OF MATING ON MALE. 1. Gradual exhaustion due to successive matings. Observations of several authors have shown that successive matings cause gradual exhaustion of the given ♂. This exhaustion may be found in the gradually lower supply of sperm. A gradually lower supply of sperm means that it is sooner exhausted by the ♀ and a higher percentage of ♂ progeny may consequently be found in its progeny (see: progeny and sex ratio). As examples *Aphidius matricariae* (VEVAI 1942), *A. smithi* (WIACKOWSKI 1962) might be mentioned.

Furthermore, gradual exhaustion due to successive matings may be recognized from gradually longer intervals between the separate matings. This was observed in *Praon exoletum* (SCHLINGER & HALL 1960). *Trioxys complanatus*, however, exhibited equal intervals between the successive matings (SCHLINGER & HALL 1961).

A third result of successive matings may be seen in the relative length of separate matings. In *Praon exoletum*, according to observations of SCHLINGER & HALL (1960), the length of separate matings was gradually longer: in the ♂ which gradually mated 10 different virgin ♀♀, the first union lasted 15 sec and the 10th union lasted 24 sec. On the contrary, the length of separate gradual matings was found to be gradually shorter in *Trioxys complanatus* (SCHLINGER & HALL 1961): in a single ♂, the length of mating with the first virgin ♀ was 12 sec, while it lasted merely 3 sec in the case of the ninth ♀.

Finally, longevity of ♂♂ seems to be also dependent on the degree of their mating activity and corresponding exhaustion.

2. Copulation attempts male—male. Parasite ♂♂ of various species, in laboratory rearings namely, may commonly be observed trying to "copulate" with another ♂. Apparently the copulation instinct is stronger than that of distinguishing a ♀.

According to the observations of SEKHAR (1957) made on *Praon aguti*, such a case occurs when one of the ♂♂ has just finished a successful act of copulation. The remains of the female odour would seem to cause the stimulation of other ♂♂, resulting in copulation attempts, the search for ♀ odour being again the primary stimulus, overruling that of the corresponding behaviour of a virgin ♀.

3. "Simultaneous" matings. If a higher number of parasite ♂♂ is present, a ♂ can be observed to mount a ♀ and copulate normally, but another 2–3 ♂♂ mount the first ♂ and try to copulate as well. Although only a single ♂, the first one, is actually copulating, the whole group of ♂♂ appears to copulate simultaneously before being examined in detail.

- PARTHENOGENETIC POPULATIONS OR STRAINS. In thelytokous populations or strains there is a total absence of ♂♂, so that there is no mating problem at all. In deuterotokous populations, however, a certain number of ♂♂ can be found among the ♀ progeny. Although no detailed information is at hand, it is not clear whether such ♂♂ even exhibit mating activity, or whether they have any role in a ♀'s behaviour or not as the deuterotokous type of reproduction means the occurrence of ♂♂ to have an accidental character.

- BIOLOGICAL CONTROL. There is no surplus ♂ problem in the aphidiids owing to the mated ♀'s behaviour. As mentioned earlier, the mated ♀♀ lose their typical odour and this prevents them from being found by the searching ♂♂, except for accidental meetings; further, they actively repel the searching ♂ and refuse to be mated for the second time. Consequently, a surplus sperm supply with corresponding influence as to the ♀ action cannot be observed. A too high number of ♂♂ may perhaps cause certain difficulties in laboratory mass-rearings as the ♂♂ searching for ♀♀ may stimulate the host aphids present; in certain cases, such as in *Acyrtosiphon pisum*, the aphids can stop feeding, fall down from the plants, etc., and this repeated stimulation may result in poor quality of host aphid rearings.

In certain aphid species deuterotokous or thelytokous populations may be found in various parts of their distribution area. The above mentioned review of factors discloses a certain number of disadvantages. These disadvantages can be seen also if the parasite species are used as biological control agents. Parthenogenetic populations or strains of parasites do not exhibit such negative features and selection of such races has to be kept in mind in a parasite introduction program.

REFERENCES. 23, 98, 294, 354, 384, 486, 497, 679, 681, 762, 1003, 1005, 1022, 1023, 1039, 1062, 1101, 1111, 1121, 1125, 1142, 1158, 1231, 1254, 1285, 1295, 1299.

Progeny, Sex Ratio

Progeny and sex ratio represent one of the important phenomena for the understanding of the effectiveness of the aphidids under various conditions. Sex ratio is a dynamic phenomenon, one of the results of the influence of environmental conditions on the parasite species. These relations of the species and the environment are often rather complicated.

- TYPES OF REPRODUCTION. Aphid parasites are members of the Hymenoptera, which are characterized by the parthenogenetical type of reproduction. We can distinguish three groups of parthenogenetic reproduction in the parasitic Hymenoptera, i.e. thelytoky, deuterotoky, and arrhenotoky. All these types were also ascertained in the aphidids.

- Arrhenotoky - The eggs can develop either parthenogenetically or zygogenetically, depending upon the occurrence of fertilization. In these cases the fertilized eggs are diploid and give rise to ♀♀, whereas the azygotes from unfertilized eggs are haploid and are ♂♂. In the arrhenotokous species the ♀♀ are normally biparental and the ♂♂ are uniparental (DOUTT, 1959). Besides its common occurrence as a result of the unmating of the ♀, arrhenotoky can also take place due to oviposition before mating, unsuccessful mating, higher age of the ♀ and temperature conditions (high or low temperatures, cold storage, etc.).

Arrhenotoky is a phenomenon that has been ascertained widely, as occurring in the aphidids, by various authors: *Aphidius ervi* (STARÝ, 1962), *A. meqourae* (STARÝ 1964), *A. smithi* (WIACKOWSKI 1962), *Diaeretiella rapae* (HAFEZ, 1961, BROUSSAL 1962, SEDLAG 1964), *Ephedrus persicae* (STARÝ, 1962), *Lysaphidus platensis* (MILLAN, 1956), *Monoctonus crepidis* (GRIFFITHS, 1960), *Praon caletum* (SCHLINGER & HALL, 1960), *Trioxys complanatus* (SCHLINGER & HALL, 1961), and others.

- Deuterotoky - is characterized by the occurrence of exceptional ♂♂. Here again the individuals are all uniparental (DOUTT, 1959). Deuterotoky seems to be relatively rare among the aphidids. The only case known seems to be that of *Lysiphlebus fabarum* in C. Europe (STARÝ, 1966).

- Thelytoky - or obligatory parthenogenesis, is characterized by the presence of only ♀♀ in each generation. Species of which ♂♂ are virtually unknown are thelytokous in the strictest sense, and all individuals are uniparental (DOUTT, 1959). Thelytokous populations in aphidids were recognized in the following species: *Lysiphlebus ambiguus* and *L. fabarum* in Israel (ROSEN 1967), *Ephedrus persicae* in California and in Far East Asia (STARÝ & SCHLINGER 1967). In all these species thelytoky is apparently a feature of race, strain or population value as the ♂♂ are known to occur in other districts of their distribution area. *Lysiphlebus desertorum* must be mentioned (STARÝ 1965), but the occurrence of thelytoky in this species has been derived from a single numerous reared series of individuals and it may not be true for the entire species.

Obligatory thelytoky is mentioned as causing changes in the anatomy of the reproductive organs. For example, *receptaculum seminis* is reduced (VOLKOV 1959). A detailed anatomical study of thelytokous aphidiids has not yet been undertaken. - Unclear cases - WEBSTER (1909) and later WHITING (1918) mentioned that ♀♀ may occasionally be found among the ♂ progeny of virgin ♀♀ of *Lysiphlebus testaceipes*. These observations must be put to question as SIKHAR (1957), working with the same species, did not have similar findings.

- *Geographic distribution*. Arrhenotokous reproduction is characteristic for the aphidiid group, occurring throughout the complete distribution area of the group while thelytoky and deuterotoky are phenomena that seem to be typical for certain strains, races or populations. For example, *Ephedrus persicae* is an almost cosmopolitan species, which is palaearctic in origin. In Europe it is an obligatorily biparental species and a similar situation seems to occur in C. Asia. In the Nearctic region, as far as it is known, ♂♂ are recorded only from Canada, while the species is thelytokous in California. In Far East Asia it is a thelytokous species (STARÝ & SCHLINGER 1967). As another example *Lysiphlebus fabarum* may be mentioned. This species is biparental and deuterotokous in Europe and C. Asia (STARÝ 1965, 1966), while it is thelytokous in Israel (ROSEN 1967). Similarly, *Lambiguus* is biparental in Europe and C. Asia, but it is mentioned to be thelytokous in Israel by ROSEN (1967).

- *Phylogeny*. If all the groups are dealt with there is no doubt that arrhenotoky is a preponderant type of reproduction. It is, therefore, a type of reproduction that has been typical for the groups during its evolution. The occurrence of thelytokous and deuterotokous populations, races or strains, which can mostly be found in widely distributed and widely specialized species, seems to show certain developmental trends. The reason as to why they have appeared has not yet been satisfactorily explained as simultaneously with such thelytokous or deuterotokous species, there occur other parasite species of normal biparental reproduction. Consequently, we cannot derive the first mentioned type of reproduction as being typical of a climatic zone or aphidiid group.

- *Aphids and parasites*. Aphids exhibit quite a number of types in reproduction, which may be simple to very complicated. Sexual and parthenogenetic progeny often alternate. In the temperate zone, a parthenogenetic type of reproduction is typical of the favourable period of the year, while the winter is spent in the egg stage. Moreover, climatic changes in the past have influenced the original life-cycles of the aphids and we can find today various populations exhibiting different types of reproduction in various parts of the distribution area of the species. Further, it is typical of the aphids that sexual reproduction is reduced in the tropics, where parthenogenetic progeny exclusively may be found.

Contrary to aphids, the aphidiid parasites show their own features. These features only stress the taxonomical difference of the parasites, which is just typical in adult stage. Reproduction in the parasites is one of the characters that clearly shows us the difference between host and parasite groups and restricted significance of phylogenetic parallelism. The aphidiids, in general, are arrhenotokous. There are no seasonal alternations of sexual and parthenogenetic progeny in the parasites. Thelytoky or deuterotoky are on a level of races to populations. With respect to their North-south distribution, the parasites do not exhibit changes of an arrhenotokous type of reproduction; arrhenotoky can be found both in temperate and tropical regions.

- *SEX RATIO*. Sex ratio is a dynamic phenomenon. It is determined through the peculiar mechanisms of the parasite ♀, which respond to the stimuli of extrinsic factors.

The majority of records which may be found in the literature and those based on occasionally or seasonally taken field or laboratory samples show general data on the ratio of ♀♀ and ♂♂. Such general data do not reveal any mechanisms of the sex ratio regulation nor the factors that influence it.

ARTHUR (1944)—*Aphidius avenae*, slight preponderance of ♀♀ in field samples; BEIRNE (1942)—*Praon volucre*, slight preponderance of ♀♀ in field samples; BODENHEIMER & NEUMARK (1955)—*Pauesia* sp., equal numbers of ♂♂ and ♀♀ in field samples; DUNN (1949)—*Aphidius avenae*, slight preponderance of ♂♂; HAFEZ (1961)—*Diaeretiella rapae*, slight preponderance of ♀♀ throughout the season; MILLAN (1956)—*Lysaphidius platensis*, preponderance of ♀♀; SCHLINGER, HAGEN & V.D. BOSCH (1960)—*Trioxys pallidus*, sex ratio 1:1; STARÝ (1964)—*Aphidius megourae*, sex ratio 2:1 in laboratory rearings; STARÝ (unpublished)—*Lysiphlebus testaceipes* in Cuba, sex ratio 2:1 in various field samples.

— *Mechanisms*. According to FLANDERS (1946, 1952; DOUTT 1959) the spermatheca becomes a sex changing mechanism when it contains spermatozoa. The sex of the egg is determined during oviposition, and the stimulation of the spermatheca to discharge spermatozoa into the oviduct is usually brought about by external conditions. As the environmental factors are inconstant, the sex ratio is variable as a consequence. Sperm that is stored in the spermatheca of the mated ♀ is believed to be quiescent and must be subjected to some activating agent before migrating down the sperm duct to fertilize an egg. The source of the activating agent appears to be the spermathecal gland, which apparently is responsive to external stimuli.

— *Factors*. 1. Successive matings. Several authors have recognized that the supply of sperm is gradually exhausted because of successive matings; in consequence, ♀♀ in the first or second mating of a ♂ exhibit a preponderance of ♀♀ in progeny, especially during the first days after mating, while ♂♂ preponderate in the progeny of ♀♀ that were mated later by the same ♂. Several examples may be mentioned: VEVAI (1942) found that in *Aphidius matricariae* in early matings, the ♀ offspring predominated but in later matings the sex ratio of the progeny was approximately equal. SEKHAR (1957) ascertained a similar situation occurring in *Praon aguti* and *Lysiphlebus testaceipes* (Table 1). According to SCHLINGER & HALL (1960) ♀♀ of *Praon exoletum* that were the first matings of a ♂ usually produced progeny in a sex ratio 1:1, with successive matings the number of ♂ progeny increased, so that a ♀ that was seventh in a series to be mated by one ♂ produced 58 ♂♂ and only one ♀. They (1961) ascertained a similar situation in *Trioxys complanatus*, ♀♀ that were the first or second matings of a ♂ usually produced progeny in a sex ratio 1:1; a ♀ that was ninth in a series of matings by a single ♂ produced progeny in the ratio of 49 ♂♂ to 2 ♀♀. The sex ratio with respect to successive matings was as follows in *Aphidius smithi*: (WIACKOWSKI, 1962): First mating 72% ♀♀, second 33%, third 35% and the fifth 40%.

Therefore, if sex ratio with respect to successive mating is to be determined, records on the first or second mating must be considered as the most correct, freshly emerged ♀ and ♂ parasite adults being taken in an experiment.

2. Times of mating and emergence. According to WIACKOWSKI (1962) the most favourable time for mating in *Aphidius smithi* is the first 24 hours after emergence, the ♀ usually mating on the same day as it emerges, or within 24 hours after. It was only rarely that the ♀ mated two days after emergence, while copulation was never observed on the third day after the emergence of the ♀.

3. Rate of mating. A successful mating must last a given period of time which is specific, otherwise—if shorter—the mating is incomplete and ♂♂ exclusively are produced as a result. For example, see WIACKOWSKI (1962) (p. 68).

4. Beginning of oviposition. If oviposition is started before a ♀ is mated, she

Female No.	Average Number of Offspring per Female			
	L. testaceipes		Pr. aguti	
	♂	♀	♂	♀
1	33	71	9	52
2	26	91	13	60
3	20	81	13	57
4	25	66	18	52
5	25	46	24	51
6	43	61	14	24
7	21	27	16	25
8	30	32	19	31
9	43	44	31	24
10	88	86	39	48
11	94	77	29	43
12	93	81	30	48
13	104	97	30	34
14	36	29	31	43
15	34	28	44	35
16	67	63	25	18
17	60	57	32	29
18	20	19	33	37
19	19	21	37	33
20			58	55
21			36	38
22			26	30
Average per female	47.6	60.6	25.8	40.5
Total offspring	2999	3818	1781	2799

Table 1. The relation of order of mating to the sex ratio of the progeny from four males each of *Lysiphlebus testaceipes* and *Praon aguti*. (SEKHAR, 1957).

refuses to be mated when a ♂ appears later on, ♂ progeny being produced in consequence (SUBBA RAO & SHARMA, 1962, *Trioxys indicus*).

5. Rapidity of oviposition. Each normal oviposition requires a certain period and also the act of oviposition must be separated by certain minimal intervals from each other if the egg is to be fertilized. When the eggs are laid too rapidly, for example due to concentrated oviposition stimuli because of the long absence of the host, the mechanisms of the ♀ apparently need a somewhat longer period to come to a proper function, so that unfertilized eggs are produced in spite of good mating and a spermatheca full of sperm. On the contrary, if the intervals of the host absence are short, the eggs are mostly fertilized (WIACKOWSKI 1962, *Aphidius smithi*).

6. Age of parasite female. When a fertilized ♀ is younger she produces fertilized eggs, while in older ♀♀ unfertilized eggs are in preponderance. This is due to the gradual exhaustion of the sperm supply in the ♀'s spermatheca; this supply cannot be completed by another mating as a ♀ mates only once in her life. Experiments of VEVAI (1942) (Table 2), SEKHAR (1957) and MESSENGER & FORCE (1963) are illustrative. In the progeny of ♀♀, therefore, it is necessary to distinguish the over-all sex ratio and the sex ratio of ♀ progeny at different periods of her life.

7. Superparasitism. Sex ratio may be also influenced by competition of the larvae

No. of sessiles obtained at 3-day intervals

Female	1		2		3		4		5		6		j	
no.	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
1	8	33	10	41	18	16	19	5	8	3	—	—	—	—
2	8	55	5	22	9	25	2	19	5	18	3	1	—	—
3	4	18	1	12	2	3	0	1	—	—	—	—	—	—
4	3	16	1	12	4	15	—	—	—	—	—	—	—	—
5	4	12	6	7	5	6	1	4	—	—	—	—	—	—
6	15	38	19	26	13	13	12	3	—	—	—	—	—	—
7	7	7	11	10	1	6	2	0	—	—	—	—	—	—
8	4	17	10	10	2	3	—	—	—	—	—	—	—	—
9	8	8	8	12	2	3	—	—	—	—	—	—	—	—
10	7	12	6	22	8	15	8	16	17	7	—	—	—	—
Total of both sexes	284		251		169		92		58		4		0	
Ratio ♂:♀	1:3.17		1:2.26		1:2.26		1:1.09		1:0.93		1:0.33		—	

Table 2. Records of sessiles and progeny obtained from single mated females. *Aphidius matricariae* (VEVAI, 1942).

in a single host (SALT, 1961). This does not seem to be the case of the aphidiids, as the oldest larva survives irrespective of its sex ratio (see: Intraspecific relations).

8. Longevity. As was previously mentioned, ♀♀ do not mate in later periods of their life, although ♂♂ may be present. It seems that ♂♂ can mate throughout their life.

9. Food. The same food is accepted both by ♀♀ and ♂♂. It does not seem to have any significance on the sex ratio. Adults may even mate and oviposit without accepting any food during the first short period of their life. Perhaps, the only part food plays may be in that when food is accepted the longevity is longer and allows a ♀ to deposit all her supply of eggs if hosts are available, while mated but not fed ♀♀ probably deposit only a certain part of their egg supply; as the fertilized eggs are laid first due to the supply of sperm in a ♀'s spermatheca, it is probable that the sex ratio could be influenced through food in this way. Experimental proof is necessary.

10. Dispersal. According to V. D. BOSCH ET AL. (1966) the exclusive occurrence of *Aphidius smithi* ♀♀ in the adult parasite catches during the first two weeks following resumption of samplings (Fig. 235) indicates that wasps had entered the field under their own power, since some of these carried into the field by parasitized aphids would most probably have been ♂♂. As we mention in the paragraph on dispersal, it is highly improbable that there would occur a similar difference in the mode of dispersal of ♂♂ and ♀♀; host mist preference of a parasite ♀ is a further proof. However, there is no doubt that parasite ♀♀ exhibit apparently a greater active dispersal when searching for hosts in the new environments. Consequently, sex ratio in the old and new plot must be compared in order to understand the first situation in sex ratio in a new plot.

11. Mortality. Sex ratio can also be influenced by the different mortality of the sexes during development (WACKOWSKI, 1962).

12. Host species preference. In some parasitic Hymenoptera, fertilized eggs are laid in suitable hosts, while unfertilized eggs are laid in unsuitable ones (FLANDERS 1965). We have no records on this factor in the Aphididae.

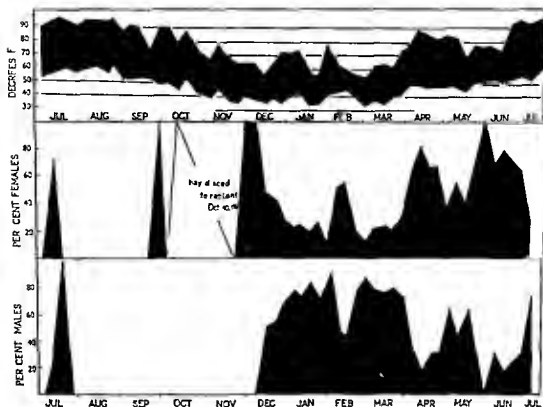


Fig. 235. Weekly mean maximum and mean minimum temperatures and sex ratios of *Aphidius smithi* in an alfalfa field at Riverside, California, July 1961 to July 1962 (V.D. BOSCH et al., 1966).

13. Host instar and form preference. Host instar and form does not seem to have any relation to the regulation of sex ratio (STARÝ 1962).

14. Host density has a great influence on parasite sex ratio. When there is a high host population density, the ♀ lays the eggs rapidly and a large number of unfertilized eggs is consequently included in this number: ♂ progeny therefore predominates in the succeeding generation. When the host population is more scarce, the ♀ must search for the host for a certain period and its progeny consequently includes more fertilized eggs. This influence of the density was well demonstrated in laboratory conditions on *Aphidius smithi* (WIACKOWSKI 1962). It may be also observed from the field data as mentioned by V. D. BOSCH et al. (1966) (Figs. 235).

15. Parasite density. When the parasite density is high, there is a greater possibility of both sexes meeting. Under a too low parasite density this probability decreases. The searching ability of the ♂♂ plays a role as well.

16. Temperature. Extreme temperature conditions both near the lower and upper thermal limit result in the apparent preponderance of ♂♂ in the progeny of fertilized ♀♀. This is due to the inability of mating. Copulation may be observed to occur under such conditions and it is possible that the sperm is not transferred, or the sperm is not viable, or sperm is not able to pass from the spermatheca to the eggs as they pass through the oviduct (MESSENGER & FORCE 1963; FORCE & MESSENGER 1964, *Praon evaletum*; WIACKOWSKI 1962, *Aphidius smithi*).

17. Season. Sex ratio may or may not fluctuate considerably during the season. According to SEDLAG (1959, 1964) a preponderance of ♀♀ was perennial in *Diaeretiella rapae* in Germany. HAFEZ (1961) ascertained a decline in the sex ratio of ♀♀ in winter

- *Main types.* Although a general scheme of the oviposition act is the same for the whole group, a more detailed study of the oviposition act in separate genera and species shows that there are many differences. For this reason, we have selected some species in which the oviposition act is well known to demonstrate these differences. It is believed that a more detailed research of the oviposition behaviour of separate species will bring us more information on this significant phase of their life.

A comparison of the main features of oviposition behaviour clearly shows that there can be certain common features for members of a separate genus, which may be given morphologically (*Trioxys*) or not (*Praon*), or differences may be found also in the different species of the same genus, etc.

The examples are dealt with only in respect of the details in which they differ from the general scheme of the oviposition act mentioned earlier.

Ephedrus persicae. The oviposition behaviour seems to be of a normal type. Length of oviposition 10-15 sec. The attacked *Myzus cerasi* tried to repel the attacking ♀ by movements of legs or by running away, but the ♀ bent the abdomen accordingly or followed the running aphid, the ovipositor remaining inserted (STARÝ, 1962).

Praon exoletum and spp. When contact is made with *Therioaphis trifolii*, the ♀ stops quickly and slightly taps her antennae on the back of the aphid. Then she usually puts her front legs (or, more rarely, her middle legs) on top of the aphid and elevates herself by quickly straightening up her hind legs. Then she bends her abdomen downward and forward, so that the ovipositor sheaths extend beyond her head, and oviposits in the aphid. Stinging is effected by a very rapid thrust of the ovipositor. Length of the act is less than 3/10th of a sec (SCHLINGER & HALL, 1960).

The placing of the fore legs on the attacked aphid seems to be typical of *Praon* species. SCHLINGER & HALL supposed this to be an adaptation to overcome the jumping habit of the aphid; however, similar behaviour was observed in *Pr. volucre* attacking *Hyalopteris pruni* by BEIRNE (1942), but this aphid does not exhibit a jumping habit. *Pr. aguti* showed a similar behaviour when attacking non-jumping hosts (SEKIJAR 1957). Consequently, this behaviour is apparently a general adaptation for more successful oviposition in *Praon*-species. It seems to be a similar one in function as the role of prongs in the *Trioxys*-species.

Aphidius ervi. Increasing antennal tapping of the ♀ can be observed during oviposition. She oviposits with her wings put on her back. Only if the aphid tries to escape, she pursues it in the oviposition posture, flapping her wings, apparently to quicken her movements. Length of oviposition act is about 1 sec. The continuous antennal tapping seems to be an adaptation to quick escape reactions of the aphid (STARÝ 1962).

Aphidius megourae. When searching for the host the ♀ holds her antennae forward and slightly bent downward. If an aphid is tapped (*Megoura viciae*) the antennae are held upwards and the oviposition posture follows. The awaiting position before the act is as follows: the ♀ stands on erected legs, the abdomen bent downwards. The true oviposition posture is similar, only the bent abdomen is stretched forwards, moving until the host is tapped by the end of the ovipositor sheaths. The sting and oviposition follow, lasting 1.2 to 1 sec. Wings of the ovipositing ♀ are laid in a horizontal position. If the aphid changes its position after being tapped by the antennae and before it was stung, the ♀ moves her abdomen searching for the aphid and only afterwards the macro-orientation sets on again. More rarely, the ♀ follows the moving aphid with abdomen bent forward, usually in the cases when she tries to sting the aphid for the second time. Judging from the general oviposition behaviour of the ♀ it is apparent that the primary orientation or macro-orientation is made by using the antennae, while the secondary orientation or micro-orientation is made by the setae on the

ovipositor sheaths. The latter is apparent also from the movements of abdomen when a ♀ searches for the aphid (STARÝ, 1964, 1966).

Aphidius transcaspicus. After *Aphis craccivora* (unnatural host) is tapped by the antennae, the ♀ holds her antennae upward. Then the abdomen is bent under the thorax and flapping of wings may be observed. The wings then are held in quite the same position and the sting follows. Several strikes can often be observed if the ♀ does not meet the aphid, the last one being the sting and apparently an egg deposition as well. Length of the act is approximately 3/10ths of a sec. The oviposition behaviour in the case of an attack on a natural host, *Hyalepterus pruni*, seems, in general, to be the same.

Diactetiella rapae. After contact with the host aphid (*Brevicoryne brassicae*) is made, the abdomen of the ♀ is bent anteriorly beneath the thorax and between the legs to reach well in front of her head. The ovipositor is then inserted with a quick movement and an egg is deposited. Length of the act is less than 1 sec. Thus, in most cases, the ovipositing ♀ remains within some distance of the host and contacts it only with the ovipositor (HAFEZ, 1961, SEDLAG, 1964, WILBERT, 1967).

Lysiphlebus fabarum. According to observations of TREMBLAY (1964) the ovipositing ♀ continually taps both the surface and the host aphid with her antennae. Length of the act is from 55-60 sec to 2 min. According to our observations the first orientation in an aphid (*Aphis fabae*) colony is made by the antennae, but later the aphid moves with the abdomen bent forward and often oviposits into the aphids without tapping them by the antennae. The latter might be a specific feature of this species which is a typical parasite attacking aphids that live in dense colonies.

Monoctonus crepidis. When a ♀ attacks a suitable individual of *Nasonovia ribis-nigri*, she approaches it, examines it with the antennae, reaches forward to grasp it with the fore legs, and, with a swift motion, bends her abdomen forward and under. With a forward thrust she inserts her ovipositor into the ventral surface of the aphid in the transverse suture between the first and second pairs of legs. Length of the act is 13-20 sec. During the act the ♀ holds the wings extended behind her, all the while retaining its hold on the aphid with her fore legs and standing antero-lateral to the host. She then withdraws her ovipositor until it is a fraction away from the aphid's body, pauses in this position for a few moments, straightens her abdomen and finally releases the aphid (GRIFFITHS, 1960). The holding of the aphid with the fore legs and specific oviposition site seem to be the most characteristic for this species.

Trioxys complanatus. When a ♀ approaches an aphid, she raises her wings to a vertical position and rapidly vibrates them. When contact with the aphid is made, the parasite quickly strikes it with the ovipositor in the manner of other aphidius. Only the ovipositor and ventral prongs touch the aphid during parasite position. If the ovipositor is not inserted the parasite backs away and moves around the aphid to another position; or occasionally, she strikes it again in the same area. Even though the ovipositor has evidently been inserted, the ♀ often continues to strike again and again (SCHLINGER & HALL, 1961).

The ♀♀ of *Trioxys* species show an apparent morphological adaptation to ovipositing in aphids (see below). The purpose of their accessory prongs acting as an opposite to downward curved ovipositor sheaths and ovipositor is apparently to hold the aphid attacked and prevent its escape. This function of the apparatus is the same, whether the *Trioxys* species attacks the jumping or non-jumping aphids. (Fig. 236).

Metaphidius aterrimus. ♀♀ of this species are adapted morphologically similarly as the *Trioxys* species as to the function of the accessory apparatus, but in this case

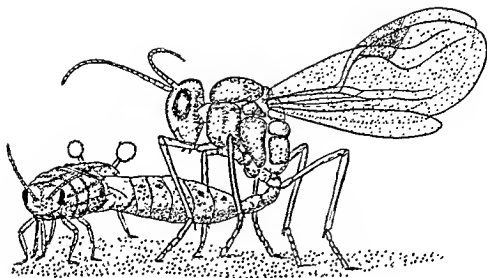


Fig. 236. Oviposition of *Trioxys angelicae*. Aphid: *Aphis pomi* (EIDMANN, 1924).

there is a tubular prong developed at the base of the seventh abdominal tergite, the ovipositor sheaths and ovipositor being curved upward and acting as an opposite to the prong.

- *Oviposition site.* An egg can generally be deposited in any part of the host body, but certain parts may be preferred or specific as an oviposition site. Two main groups can be recognized among the parasites in this respect:

- Various parts of host body - *Aphidius matricariae*: out of 852 strikes observed, 14.9% were made from the front, 30.7% from behind, 54.4% from the side of the host. The favourable site is that part of the abdomen in the region of cornicles (VIVALI, 1942). *A. megourae*: the ♀ stings in any part of the host body, but usually in the abdomen. Only if higher instar aphids are attacked, the stings in legs are common (STARÝ, 1964). *A. transcaspicus*: the ♀ oviposits mostly in the abdomen of the host. *Lysiphlebus fabarum*: the host is mostly stung in the abdomen. *L. testaceipes*: the ♀ mostly oviposits in the ventral part or sides of the host's abdomen, then between the cornicles, in head, thorax and legs, and most rarely in the antennae (SEKHAR, 1957). *Praon aguti*: the ♀ oviposits mostly in the ventral part of host's abdomen and between the cornicles, then in the sides of the abdomen, then in head, thorax, and rarely in antennae and legs (SEKHAR, 1957). *P. exoletum*: the ♀ does not orient itself to sting any particular part of the aphid, but rather oviposits in the aphid from whichever angle is approached. Most of the stings occur in the abdomen (SCHLINGER & HALL, 1960).

- Specific parts of host body - In *Monostonus trepidis* the site for oviposition is usually very precise, and, should the parasite first contact the aphid from behind, it swings around rapidly into a position from which it can insert its ovipositor anteriorly, into the ventral surface of the aphid in the transverse suture between the first and second pair of legs. Later observation proved that the deposition of an egg in any other place was of rare occurrence, and was only observed when the parasite was attacking large, active aphids (CHRISTIAN, 1960).

- Factors - 1. Host instar. Every parasite species has a host instar which it prefers when ovipositing. However, generally all the host instars may be attacked, so that

the ♀ attacks also less suitable instars. The latter case seems to exhibit also an influence on the oviposition site. In *Aphidius megourae* the ♀♀ often oviposited in host's legs, while this was not the case of preferred low instar aphids (STARÝ, 1964). Similarly, when the ♀ *Monoctonus crepidis* attacked large aphids, she was unable to deposit eggs in the specific area (GRIFFITHS, 1960).

2. Angle of parasite attack. A ♀ may approach the aphid from different angles. In some species such as *Praon exoletum* or *Trioxys complanatus*, the angle of attack has no significance as to the oviposition site (SCHLINGER & HALL, 1960, 1961). In other species, such as *Aphidius matricariae*, the angle of attack is important, the parasite usually avoiding the posterior abdominal segments possibly because there is a risk of making contact with the honeydew of the host (VEVAI, 1942). Or, in a particular case, the ♀ must attack the aphid from a certain given angle to oviposit in a specific area; this is the case of *Monoctonus crepidis* (GRIFFITHS, 1960) (see below).

3. Intrinsic features. Some species, such as *Monoctonus crepidis*, deposit their eggs in a specific part of the host's abdomen (GRIFFITHS, 1960). This behaviour does not seem to be entirely clear as the eggs deposited in any part of the abdomen, except cornicles, develop successfully, as can be observed in the whole aphidiid group.

4. Honeydew production. The angle of attack is perhaps sometimes influenced by the production of fresh honeydew by the aphid which the parasite ♀ avoids to contact (VEVAI, 1942, in *Aphidius matricariae*).

5. Waxy covers. In many aphid species there are waxy covers developed to a various degree. As the parasites generally avoid coming into contact with the wax, it is possible that parts of the host's body where less wax covers are to be found are preferred.

— Significance for egg development — The oviposition site has a basic significance as to the further development of the laid eggs. Observations of several authors showed that few progeny were obtained from thoracic strikes (SEKHAR, 1957), while no progeny developed from strikes in antennae, head, cornicles, legs (SEKHAR; VEVAI, 1942). Apparently, the eggs deposited in these parts fail to develop because of a too restricted space, while the common oviposition site—the abdomen—enables the laid eggs to develop normally with no dependence whatever which part of the abdomen was oviposited in.

— Host paralysis. The parasitic Hymenoptera may or may not paralyze or kill their host prior to oviposition (POUTT, 1959). Anatomical studies of the reproductive system of the aphidiids have shown that there are probably poison glands at least in some species developed (e.g. *Trioxys complanatus*, SCHLINGER & HALL, 1961, etc.). However, the function of the poison during the oviposition act is not clear. It is apparent that the possible injection of venom to paralyze the host and the act of oviposition are a single operation being a simultaneous act. However, judging from the host's responses to parasite attack the injection of venom may or may not occur: the aphids may respond by moving their legs, by quick motions of the abdomen, escape reactions, producing a small drop of liquid from siphuncles, etc., or they may show no response to being oviposited. Their response may be also due to the sting through their integument. It is evident that further research is necessary in this direction.

The single reported record on paralysis of an aphid as a sequence of oviposition is that of TELENGA (1950) who mentioned this period of host paralysis to be as long as half an hour. However, observations of various authors as well as our own disclose contrary results.

— Number of strikes and number of laid eggs. A strike is defined as the act of the parasite whereby the ovipositor is thrust toward the aphid, with or without making contact (SCHLINGER & HALL, 1961).

The number of strikes is generally higher than the number of laid eggs. A ♀ often prepares to oviposit, but the aphid may escape and no contact follow, some ♀♀ may wait with thrusting ovipositor until the aphid moves and then they oviposit.

A most unusual manner of strikes was observed in *Trioxys complanatus*. The action of the prongs seems to explain the multiple strikes. When the strike is made and the prongs do not gain a grip on the aphid integument, the parasite has then nothing to pull against and is unable to insert the ovipositor. Therefore, if an egg leaves the ovipositor at that time, it is deposited on the outside of the aphid and is lost. The ♀ not having gained a firm hold on the aphid will strike repeatedly until the prongs become secure and give it the needed support for the insertion of its ovipositor (SCHLINGER & HALL, 1961).

— *Number of stings and number of laid eggs.* A sting is the contact of the ovipositor with the host body. A sting may or may not mean that an egg was laid. The number of stings is generally more numerous than the number of laid eggs.

VEVAI (1942) recognized experimentally that when only one sting was allowed per aphid 340 out of 1463 specimens became parasitized (23.2%), when two stings were allowed 45.7%, when three strikes 80% and 100% with four strikes. WIACKOWSKI (1960, 1962) found that the average number of actual ovipositions was one per three insertions of ovipositor in *Aphidius smithi*.

Host behaviour and parasite oviposition behaviour seem to influence the relation between the number of stings and laid eggs, to a high degree. In *Praon exoletum*, if conditions are favourable, the ♀ strikes at an aphid only once, but if the aphid moves or the parasite misjudges the angle or position of the host, it will continue to strike until the egg is deposited (SCHLINGER & HALL, 1960). In *Trioxys complanatus*, because of the habit of the ♀ not to touch the aphids with antennae before ovipositing, multiple stings are common (SCHLINGER & HALL, 1961).

— *Number of eggs per insertion of ovipositor.* As mentioned above, an egg may or may not be deposited simultaneously with the insertion of the ovipositor. The state of the ♀, i.e. whether she is present all the time near the host and has no concentrated oviposition urge due to a temporary lack of host, a single egg may be laid almost at each insertion (STARÝ, 1964, *Aphidius megourae*, ULLYET, 1938, *Diaretiella rapae*).

A particular case seems to be that of *Trioxys complanatus* as described by SCHLINGER & HALL (1961). It is thought that when several eggs are deposited with a single insertion of the ovipositor it is because the wasp is unable to release the grip of the prongs immediately. The deposition of several eggs under these circumstances usually occurs more frequently in older aphids (instar IV or adults) which have a much thicker or tougher integument than the younger ones, and the prongs are released with greater difficulty; 2–3 eggs are usually deposited under these conditions, but as many as 10 can be found.

— *Post-oviposition behaviour.* An oviposition act is finished by the retraction of the ovipositor and straightening of the abdomen to a normal position. After finishing one oviposition act, the ♀ can immediately search for another aphid, or it may spend a certain time in a so called resting period, when she cleans herself, slightly strikes her abdomen with the hind legs, strokes her antennae between the fore legs and mouthparts, she may feed, or sit motionless on a leaf, etc. Post-oviposition behaviour, especially the frequency and length of the resting period, is determined by the intensity of oviposition and the age of the ♀ (see below). The resting period is characterized by the parasite ignoring the host.

— *RAPIDITY OF OVIPOSITION.* Oviposition does not generally exhibit the same rapidity during the whole life of the parasite. Usually, a ♀ oviposits in a certain series of hosts, then rests, another series of oviposition acts follows, a resting period, etc.

The resting periods are gradually longer depending on the ♀'s age and oviposition intensity. The maximum number of eggs, in a host's presence, are laid during the first few days of the parasite lifetime.

Praon exoletum (SCHLINGER & HALL, 1960). Oviposition usually takes place in rapid succession in groups of 6 to 16 stings, provided that hosts are available. The ♀ then enters a rest period of about 5–30 min, during which time there are no signs of any ovipositional attitudes. When she is ready to sting again she repeats a similar group of stings before resting again. The number of stings in successive series gradually diminishes, until near death there is a rest period of about 45 min and as few as six stings are noted. Towards the end of each sting period the rapidity with which the ♀ stings slows down considerably after contact is made. After a ♀ locates the aphid, she often elevates herself and thrusts her abdomen forward as if to oviposit, but does not touch the aphid with the ovipositor. ♀♀ were observed to remain in this position for as long as 30 sec before slowly moving the ovipositor towards the aphid and ovipositing; movement of the aphid had a stimulating effect at that time.

— EGG DISPERSAL. Each parasite species has a certain pattern in behaviour in egg dispersal that may be recognized if a single ♀ oviposits in a normal colony of its host.

Some species show rather a dispersive pattern in egg deposition. They oviposit in an aphid, then run off and attack another aphid in another colony, etc. Such a behaviour can sometimes be due to the response of the aphid to parasite attack as after retracting the ovipositor from an aphid the parasite moves and runs a little so that parasitized aphids can never be found in dense groups (*Praon abjectum*, *Ephedrus plagiator*). Other species attack suitable host aphids quietly and gradually and the whole colony may be heavily parasitized in consequence (*Lysiphlebus fabarum*).

A typical parasite ♀ behaviour may be obscured by the simultaneous or gradual action of several ♀♀, by the scarcity of suitable host instars, by aphid density and by the density of aphids in a colony. The type of aphid colony is either specific or it may change during the existence of the colony. For example, GEORGE (1957) found different degrees of parasitization of *Brevicoryne brassicae* by *Diaeretiella rapae* in the upper, middle and lower leaves. On the upper leaves, the colonies of aphids are small and diffuse, the parasite does not need to search for suitable hosts. However, on the middle and lower leaves the aphid colonies are more dense and oviposition is restricted to individuals at the edge of the colony, where there is no danger of the parasite coming in contact with wax and honeydew.

— MORPHO-ECOLOGICAL ADAPTATION OF FEMALES to oviposition into the host are rather a significant adaptation, which determines basically the host-parasite relation. Many of them are similar as to their function, but they are apparent results of functional convergence in the aphidiid group. There is, for example, no doubt, that such clear adaptation to hold the attacked aphid between the prongs and ovipositor sheaths to enable a more successful attack and oviposition has developed independently in *Trioxys* and in *Metaphidius* species, being morphologically dissimilar, but having the same function.

Length of the oviposition act seems to be an adaptation of the general behaviour of the given aphid species. Some aphids are rather rapid, their responses to parasite attack are quick and immediate—such aphids are attacked by parasites that show rather a brief length of the oviposition act. Contrary to these, the slowly or non-responding aphids are attacked by parasite species that have a long oviposition act. Specific features may cause the same aphid species to be attacked by two parasite species, each of which has a different length of oviposition act. For example, *Aphis fabae* is attacked by *Lysiphlebus fabarum*, *Trioxys angelicae*, *Praon abjectum*, *Ephedrus*

plagiator, etc. *Lysiphlebus fabarum* has a long oviposition act, it follows the running aphid with ovipositor inserted; another parasite, *Trioxys angelicae*, uses its prongs to hold the attacked aphid, so that its oviposition act can be shorter, etc.

Some parasites hold their fore legs on the attacked aphid (*Praon*, *Monoclonus*). This seems to be an adaptation to prevent the escape of the attacked aphid, the adaptation being functionally equal to that of *Trioxys* species.

A classical example of morphological adaptations is the development of various prongs on the apical abdominal parts of parasite ♀♀. In *Trioxys* there are two accessory prongs developed at the last abdominal sternite, in the genus *Bioxys* there is a single prong developed; in *Metaphidius*, contrary to *Trioxys*, the prong is developed at the base of the seventh tergite. The principal function of these apparatus is to keep the attacked aphid between the prong or prongs and the ovipositor sheaths that operate as an opposite to the prongs.

A wide degree of morphological adaptation may be recognized on ovipositor sheaths of various genera and species. They are of a different shape and size (see Morphology).

- OVIPOSITION STIMULI AND HOST SUITABILITY. Many observations have shown that oviposition stimuli do not necessarily mean that the host is suitable for parasite development. Such observations were made both in the field and laboratory conditions.

SCHLINGER & HALL (1960) recognized that *Aphis spiraeicola* on Citrus is attacked by *Lysiphlebus testaceipes* in California, but the parasite never develops past the third instar; the oviposition into an unsuitable host is believed to be due to the simultaneous presence of a suitable host aphid. *Aphis helianthi* represented a similar case.

In the laboratory, BROUSSAL (1960) observed that when *Macrosiphoniella sanborni* is attacked as an unnatural host by *Diaeretiella rapae*, the parasite does not complete its development either.

Other examples are mentioned in host specificity and unnatural host propagation chapters.

- FACTORS. 1. Emergence. Different species show different intervals between emergence and starting of oviposition. Some species start to oviposit soon after emergence, others need more and sometimes a considerable time before being able to do so.

2. Mating. A number of authors did not find any differences between virgin and mated ♀♀ as to the onset of oviposition: VEYAL (1942) in *Aphidius matricariae*, TREMBLAY (1964) in *Lysiphlebus fabarum*, SUBBA RAO & SHARMA (1962) in *Trioxys indicus*. However, FLANOERS (1937, 1943) believes that the act of mating or the presence of sperm in the spermatheca has a marked effect on the behaviour of the ♀. This is surely true in the aphidiids with respect to the relation of virgin or mated ♀ to the ♂. Nevertheless, it seems that mating can also stimulate the oviposition ability. SEKHAR (1957): under the same laboratory conditions (25–35°C) mated ♀ *Lysiphlebus testaceipes* started to oviposit 4–85 min after emergence; similarly, in *Praon aguti*, mated ♀♀ started to oviposit in 2–70 min after mating, while virgin ♀♀ were able to oviposit about 2 hours after emergence.

3. Behaviour. The parasites show conspicuous differences in oviposition behaviour. Besides the true oviposition behaviour, the type of host colony is also important. Some ♀♀ oviposit in aphids if they occur in dense colonies, others may do the opposite. Nevertheless, as the colonies of the same host aphid may have a different density during a certain period of time, the parasite behaviour may influence also the oviposition through the suitability of the host colony.

4. Food. As mentioned earlier the oviposition stimuli are primary and they over-

rule the need for food at the early period of parasite adult life; however, at a later period, food or at least water is necessary if the oviposition has to be continued.

5. Fecundity. Oviposition is influenced by the number of eggs present in the reproductive system of the ♀. After this supply is exhausted the oviposition stops as a result, although the ♀ may live longer.

6. Longevity and age. Oviposition is usually most intensive during the first days after emergence. The length of the oviposition act is also shorter during this period. Gradually, when the ♀ is getting older, the number of laid eggs is smaller, the oviposition intensity is lower and the length of the act is longer, too.

7. Host density. Host absence for a longer time may cause a too high stimulation of the ♀ when she finds the host and consequently too many oviposition acts may be made in one host (superparasitism), etc. A high host density may sometimes force the ♀ to restrict her oviposition to the edges of a colony (*Diaeretiella rapae*), or not (*Lysiphlebus fabarum*). As is shown in the reproductive capacity paragraph, the higher host density stimulates the parasite oviposition up to a certain level.

8. Host preference. Every parasite species prefers a certain host instar; the oviposition act in this instar requires a given period of time. However, in case of the absence of this preferred instar, a parasite may deposit eggs in higher instars as well. As the higher instars are larger the oviposition needs more energy and time and it is relatively slower. Further, we have no detailed records whether the length of the oviposition act is the same in all the host species attacked or not. The other factors connected with the host, influence the ovipositing ♀ through the host specificity factors (host microhabitat, parasitized – nonparasitized host, etc.).

9. Host behaviour during a parasite attack can influence the oviposition to a considerable degree. Parasite adaptation plays an important role here. In some species, if the host starts running after being tapped by the parasite antenna, the ♀ is unable to follow it and the host escapes oviposition in this case, or they interrupt oviposition if the host aphid moves a little. In other species the ♀♀ pursue the running aphids and they can do so without interrupting oviposition, or they pursue the host to oviposit.

10. Mechanical stimuli. Oviposition may be interrupted by mechanical stimuli. The responses of a parasite to these stimuli are specific. In general, parasites of quickly moving aphids are more sensitive and the parasites of the slowly moving aphids less sensitive to a mechanical stimulus. The sensitive species break off the oviposition and fly or run off. E.g., it is enough for ovipositing *Aphidius megourae* to be touched by another aphid to interrupt oviposition and run off; *Lysiphlebus fabarum*, on the other hand, can be touched even with a pincette, not to speak of aphids or ants, and she quietly continues her ovipositing.

11. Temperature and relative humidity. The highest oviposition intensity is under optimal temperature and R.H. conditions. Under low temperature the parasites are poorly active and rarely and slowly oviposit, while too high temperatures stimulate them too much and oviposition does not occur. The influence of R.H. on oviposition was apparent in laboratory mass-rearings of *Trioxys complanatus* (FINNEY, PUTTLER & DAWSON, 1960): the parasite occurs in xerothermic habitats in nature. In the insectary, under humid conditions—60% R.H. and more—the adults spent most of their time in stroking their antennae, wings and legs rather than ovipositing, however, by the use of the ventilating unit the humidity was reduced to room level and oviposition was normal.

12. Day time. The parasites do not oviposit at night. As the parasite day activity is mostly in the morning and late in the afternoon, it is apparent that oviposition takes place in these periods of the day. BERTSE (1942) found that oviposition was most frequent in the morning in *Praon volucre*.

13. Artificial measures. In his experiments with *Aphidius smithi* WIACKOWSKI (1962) found that the smaller number of oviposition acts was in the case of ♀♀ threatened with CO₂ for about 1 min before the experiment, this being believed to be probably the result of the action of this gas.

- INFLUENCE OF OVIPOSITION ON PARASITE FEMALE. ♀♀ that have no chance to oviposit manifest a longer lifetime than ovipositing ♀♀. This is understandable as oviposition is naturally connected with loss of energy.

As we have already mentioned, oviposition prior to mating seems to prevent the mating of the given ♀.

Active oviposition is most rapid at the earlier periods of the ♀'s lifetime, while the ♀ is gradually slower until her death.

REFERENCES. 21-3, 65, 89, 158, 169, 273, 290, 294, 301, 314, 332-3, 355, 356, 372, 388, 421, 438, 448, 450, 476, 478, 483, 497, 499, 586, 591, 666, 670, 681, 762, 915, 962, 969, 1003, 1005, 1022, 1023, 1039, 1062, 1069, 1101, 1111, 1121, 1125, 1158, 1162-3, 1189, 1212, 1231, 1238, 1254, 1256, 1266, 1284, 1295, 1299, 1306, 1309, 1319, 1331.

Reproductive Capacity

Aphids are a group of insects which is characterized by an enormous reproduction and numbers that can be found to occur in nature under favourable conditions. For this reason, the research and knowledge of the reproduction capacity of their parasites represents a rather important part of parasite biology. It enables us, at least in part, to determine the role of the parasites as agents that participate in the elimination of aphid numbers in nature.

- POTENTIAL AND REALIZED FECUNDITY. Potential fecundity can be derived from the number of eggs present in the ovaries of a ♀ if she is reared in constant conditions and in a host's absence. According to SCHLINGER & HALL (1960), the number of eggs per ♀ may vary individually, but there is little difference in the number of eggs found in the two oviducts of the same ♀. Records on potential fecundity are relatively constant for a given population. Realized fecundity, which is usually derived from the number of laid eggs, or even parasitized aphids, may be influenced by a number of factors; moreover, there is also a difference between the number of eggs laid and the number of parasitized aphids, as all the eggs laid may not develop; furthermore, superparasitism also obscures the number of laid eggs; the number of laid eggs, too, may be obscured by the number of stings, number of ovipositions, and number of eggs laid per one oviposition act.

An extensive part of the records which can be found in the literature contain data on potential and realized fecundity. These data, however, being obtained both in the laboratory and field mostly, do not include records on factors which have influenced the fecundity of the parasites. The following is a list of examples of such data per ♀: *Aphidius avenae*. ARTHUR (1944): 153-382 eggs laid. ARTHUR (1945): min. 39, max. 89, average 82 ovarian eggs. QUILLIS (1929): max. 750 ovarian eggs. SKRIPTSHINSKY (1930): average 130 eggs laid, 200 ovarian eggs. *A. ervi*. MACGILL (1923): 120 ovarian eggs. STARÝ (1962): 140 ovarian eggs, average 50 parasitized aphids (18-24°C). *A. matricariae*. VEVAL (1924): min. 13, max. 300, average 93 ovarian eggs. *A. smithi*. WIACKOWSKI (1960, 1962): 40-150 mature ovarian eggs and a number of immature eggs, average 30-60 parasitized aphids. *Diaretiella rapae*. ULLYETT (1938):

300-400 ovarian eggs. SEDLAG (1958): 400 ovarian eggs, at least 207 laid. HAFEZ (1961): max. 175, min. 25, average laid 83. BROUSSAL (1966): 200 ovarian eggs. *Lysiphlebus fabarum*. QUILIS (1930): average 750, max. 1500 eggs laid (Note: Evidently a mistake due to bad conditions of cultures of aphids.). LIVSINC (1946): 23.1-219.9 par. aphids. LUZHETSKI (1960): 115-118 laid eggs. TREMBLAY (1964): 200-250 mature ovarian eggs, average par. aphids 111, 207, 180. *L. testaceipes*. WEBSTER & PHILLIPS (1912): 4-450 eggs, average 94.6 parasitized aphids, also 200-301. SEKHAR (1957): max. 254 par. aphids. *Praon exoletum*. SCHLINGER & HALL (1960): average 155 ovarian eggs (93 mature and 62 immature). MESSENGER & FORCE (1963): 300 or 162 eggs on the average depending on temperature conditions.

- PROOVIGENY AND SYNOVIGENY. In connection with the supply of eggs present in the ovaries at the emergence period and to the egg deposition, FLANDERS (1950: DOUTT 1964) divided the parasitic Hymenoptera into two groups:

Proovigenic species. Species of this group reach the adult stage with a complement of ripe eggs, deposit them in a brief period, and develop no other eggs during their life; the production of the eggs in these species is entirely from stored nutrients carried over from larval stages.

Synovigenic species. Most of the parasitic Hymenoptera belong to this group. Species of this group continue to produce eggs throughout the adult life. In these cases the production of eggs is dependent on the nutrition of the adult ♀ rather than on the metabolites retained from the immature stages. Proteins for the continuous production of eggs are supplied by feeding on honeydew, etc.

The classification of the aphidiids, whether they belong to proovigenic or synovigenic species, seems to be somewhat vague. If the presence of a given number of ripe eggs is taken as the basic difference, a certain part would belong to the proovigenic group. However, the aphidiids are known mostly to produce eggs for a greater part of their imaginal life, the number of eggs produced during their life is larger than the number of ripe eggs that are present in the oviduct at the day of their emergence, this would show aphidiids to belong to synovigenic species. But anatomical research has shown that there is, with some exceptions mentioned below, a certain given number of eggs in the reproductive system at the time of emergence of a ♀ which does not increase during the lifetime, however, this number includes both immature and mature eggs. Better to say, pro- and syn-ovigeny may be changed in dependence on photoperiod in the aphidiids.

Summarizing, the aphidiids include on the one hand the proovigenic species, on the other hand, they represent a certain intermediate group between the proovigeny and true synovigeny, owing to the following reasons:

- (1) They lay eggs for a great part of imaginal life;
- (2) the number of eggs is determined at the day of emergence;
- (3) both immature and mature eggs are contained in the reproductive organs of the ♀;
- (4) this egg supply is gradually exhausted, first the mature eggs of the nymphal origin are laid, then the mature eggs that developed from the original unmated eggs are laid;
- (5) resting period occurs between a series of ovipositions, during which a further portion of the eggs matures and gradually enters the oviducts;
- (6) to realize a total egg supply (a) host, (b) corresponding period of time and (c) food are necessary. The role of food is not clear (honeydew), whether it is accepted as a source of carbohydrates or as a source of proteins too; in every case, food or at least water are required by ♀♀ after a short period of post-emergence life or oviposition is interrupted.

(7) ovisorption does not occur; sometimes a slight reduction of the egg supply in ♀♀ with no possibility of ovipositing may be observed;

(8) the egg supply is specific and cannot be influenced by external factors (potential fecundity).

The above mentioned summary may be shown in further detail:

- Proovigenic species - TWATA (1959) found some specimens of "*Aphidius japonicus*" whose ovaries contained only 600-700 mature eggs and no immature eggs. This would appear to be a case of an apparent proovigeny, but specimens of the same species from other localities had 30 mature and many immature eggs in their ovaries, which is common in other aphidiids.

- Role of generation - BROUSSAL (1961) ascertained that ♀♀ of the first spring generation of *Diaeretiella rapae*, which emerged from overwintering mummies, lay only the supply of ripe eggs that reach a mature state before adult emergence. There is no oogenesis in this generation in the adult stage. The aestival generation of this species, on the contrary, exhibited the prolongation of oogenesis even after the pupal supply of eggs was deposited. This indicates that the kind of generation has an influence on the egg production in the adult stage.

- Role of photoperiod - According to BROUSSAL (1962) *Diaeretiella rapae* ♀♀ laid the only supply of ripe eggs that reached a mature state before adult emergence under 11 hours of light; 14 hours photoperiod, on the contrary, caused the production of eggs during adult lifetime in the aestival generation.

- Normal kind of egg production - The greatest part of aphidiids, in which the egg production is known, at least as to basic features, seems to produce the eggs in a manner which is related to the undermentioned:

Praon exoletum (SCHLINGER & HALL, 1960). Maturation of about 10% of the eggs takes place before emergence, and when the ♀ emerges, about 25% of her total complement of eggs are fully developed. The number of eggs present in the reproductive system of a newly emerged ♀ apparently constitutes the total reproductive capacity of that ♀, since a further maturation of eggs does not take place even though the number of eggs in the oviducts is greatly depleted after continual oviposition. ♀♀ which were allowed to oviposit freely for 24 hours, were dissected and found to contain from 10 to 20 developed eggs in the oviducts and no eggs in the ovarioles. The germarial end of the ovarioles had started to deteriorate. The fact that germarial deterioration is prevented by lack of oviposition was shown by an experiment in which 5 ♀♀, kept free from hosts until their death, showed by dissection that a full complement of both developed and undeveloped eggs were present and that no tissue breakdown had occurred.

Trioxys complanatus (SCHLINGER & HALL, 1961). Maturation of the eggs takes place before and after emergence. Approximately 75% of the total complement of eggs are fully developed when the ♀ emerges from the cocoon. The number of eggs present in the reproductive system of a newly emerged ♀ very closely measured the total reproductive capacity of that ♀, since it was observed that further maturation of eggs did not take place even though the number of eggs was depleted after a continuous period of oviposition. ♀♀ allowed to oviposit freely for 24 hours nearly exhausted the supply of eggs stored in the oviducts. There was no apparent deterioration of the ovarioles after all the eggs had been deposited, as was found in *Praon exoletum*.

Diaeretiella rapae (SEDLAC, 1959, BROUSSAL 1966). The state of eggs found in the ovarioles at the emergence of the adult was similar. The number of eggs was of course specific.

- OVISORPTION in parasitic Hymenoptera occurs if the synovigenic ♀ does not obtain

proteinaceous food or is unable to find a host for an extended period of time. Consequently, the ripe eggs in the ovarioles are not deposited but absorbed (FLANDERS, 1947; DOUTT, 1964). According to FLANDERS the phenomenon of ovisorption emphasizes the economy of parasitism, and this conservation of reproductive material is correlated with a high searching capacity. Such parasites are able to search in low host densities and conserve their eggs and restrict oviposition to sites suitable for the development of their progeny.

Experiments to ascertain whether ovisorption is developed or not in *Praon exoletum* (SCHLINGER & HALL, 1960) have shown that ♀♀ without available hosts retain their full complement of eggs until death, thus showing no signs of ovisorption. Experiments with *Trioxys complanatus*, in which ♀♀ were confined without hosts and food for 5 days, gave identical results (SCHLINGER & HALL, 1961).

However, the results of experiments with *Diaeretiella rapae* undertaken by SEDLAG (1964) showed the following situation in ♀ ovaries that had no possibility of laying eggs: first day 49.2 eggs, second day 228.3 eggs, third day 280.4 eggs, fourth day 261.6 eggs, fifth day 227.1 eggs, sixth day 176.6 eggs. Apparently, egg maturation took place in the first days of adult life, which is a common phenomenon in aphidiids. Nevertheless, the slight decrease in the number of eggs on the fifth and sixth days might be a slight indication of ovisorption.

WIACKOWSKI (1960) mentioned the process of a full degradation of eggs and ovarioles to occur on the 5th day after the emergence of *Aphidius smithi* in case of a host's absence. However, this process was later (1962) reclassified and mentioned to be independent of host's presence and needing cytological study.

—FACTORS. 1. Age of parasite female. The duration of the reproduction period may be equal to or shorter than the length of ♀ life; host presence is presumed to be continuous. In case that the host's presence is restricted to several days of ♀ life, the reproductive period is concentrated to these days, being then correspondingly shorter. Experiments on the relation of ♀ age and duration of the reproductive period undertaken by several authors represent a satisfactory proof (Table 3) (VEVAL, 1942, HAFEZ 1961, SEKHAR 1957).

Intensity of oviposition is generally most intensive during the first few days of the life if the host is continuously present. After these few days the oviposition sharply decreases. This phenomenon seems to be of general value for the whole group (Table 3) (VEVAL, 1942, SEKHAR 1957, MESSENCER & FORCE, 1963, HAFEZ 1961, LIVSHIC 1946, etc.). A parasite is able to deposit a certain maximal number of eggs per day, which is determined by the number of eggs present in the ovarioles (BROUSSAL, 1966). As we have mentioned, this number of eggs is the highest during the first few days after emergence. For example, in *Diaeretiella rapae*, there was a lack of host for 6 days after emergence, the supply of eggs should have been 388 eggs if compared with the ♀♀ in presence of host during this period; but the oviposition rate on the 7th day was only 118.5 eggs; to realize the whole accumulated supply of eggs another four days were necessary (BROUSSAL, 1966).

Oviposition stimuli are more intensive in younger ♀♀. In older ♀♀ they have no significance, as fecundity is reduced and the ♀♀ cannot overreach this reduced level even if the stimuli were very strong (BROUSSAL, 1966).

2. Mating. A careful comparison of the fecundity of virgin and mated ♀♀ of various species has clearly shown that differences can be found among them. Generally, mated ♀♀ show greater fecundity as compared to the virgin ♀♀. Mating, consequently, means a stimulation of fecundity.

ARTHUR (1945) ascertained the fecundity of *Aphidius avenae* mated ♀♀ to be clearly higher than in virgin ones.

♀♀	Strikes on successive days										Total Single Strikes
	1	2	3	4	5	6	7	8	9	10	
1	7	12	0	35	31	D	0	0	0	0	85
2	7	15	35	29	29	11	5	0	2	D	133
3	5	10	32	48	32	9	0	D	0	0	136
4	6	14	30	29	30	10	3	0	D	0	122
5	7	16	27	29	28	7	0	0	0	D	114
6	9	11	25	20	22	5	4	3	D	0	99
7	3	11	22	21	20	0	0	5	1	D	83
Total number of strikes											772
Average number of strikes per parasites											110.2

Table 3. Number of ovipositional strikes of ♀♀ of *Prion aguti* when allowed free access to hosts for one hour per day on successive days. (D = Dead) (SEKHAR, 1957).

BROUSSAL (1966) recognized the differences in fecundity of early spring and aestival generations of *Diaeretiella rapae*; however, in both these generations, mated ♀♀ exhibited higher fecundity than virgin ♀♀ (Table 4).

3. Food. The role of adult food is not yet clear with respect to parasite fecundity. It seems that it represents a source of energy for a ♀ to attain greater longevity and deposit the whole egg supply in case the host is present, but it also seems that it has no relation to the maturation of eggs. In any case, lack of food does not result in ovisorption. (SCHLINGER & HALL, 1961, *Trioxys complanatus*).

4. Mortality of progeny. A certain part of a ♀ progeny is reduced due to natural mortality. Progeny that die in the egg or lower instar larva stage may not be recognized and this factor can partly obscure the picture of realized fecundity.

5. Superparasitism or multiparasitism means a relative wastage of eggs as only a single larva survives from the whole number of parasite developmental stages present in a single host. Superparasitism, therefore, affects the fecundity realized and may obscure its true picture.

6. Size. There are unfortunately insufficient records on the relation of host size and parasite fecundity in aphidiids. The difference of parasite adults that emerged from various host instars will probably not be big, as the difference between the last instar and adult aphids, which represent mostly mummified stages, is not great. However, differences in fecundity may occur with respect to the size of parasite adults reared from different hosts. Widely specialized parasite species often attack various hosts which differ greatly in size and so do the corresponding progeny of the parasites that emerge from such hosts. We can only mention the difference in size of *Ephedrus plagiator* specimens reared from *Prociphilus fraxini* and those reared from *Aphis craccivora*; unfortunately, we have no records on the influence on the fecundity of different sizes of the parasite adults.

7. Host preference. There is no doubt that widely specialized species have certain hosts which are evidently preferred. It would be possible for parasites attacking less preferred hosts to exhibit less fecundity when compared with their fecundity when attacking preferred hosts.

BROUSSAL (1966) made experiments with *Diaeretiella rapae*. This parasite evidently prefers *Brevicoryne brassicae*, *Myzus persicae* being less attacked. When 10 ♀♀ of the



Fig. 237. Fecundity of *Diaeretiella rapae* in relation to various combinations of host numbers. Host: *Brevicoryne brassicae*. (BROUSSAL, 1966). — normal evolution in presence of 5 hosts, —.—.— single host present, ---- single host and 5 hosts, - - - - 5 hosts and single host.

parasite were added to an equal mixture of *Br. brassicae* and *M. persicae*, there were only 5% of the eggs deposited in *M. persicae* of the total number of 4,975 eggs; *Br. brassicae* was clearly preferred.

To recognize the influence of less preferred hosts on parasite fecundity, BROUSSAL added the same number of 10 ♀♀ to a number of *M. persicae* in pure culture; in this case, 4,999 eggs were laid; the fecundity was equal to that in the preferred host, *Br. brassicae*.

However, further experiments in this direction are necessary as host preference may also reveal a different intensity than in the case mentioned above. In some host species even a part of the parasite progeny may die because of less suitable host and this can obscure the realized fecundity of the parasite.

8. Host density. It is generally known that to a considerable degree host density influences the realized fecundity of a parasite. Theoretically, when hosts are available, ♀♀ are capable of depositing their full supply of eggs. This dependence has been mentioned by several authors (SCHLINGER & HALL, 1960, MESSENGER & FORCE, 1963, BROUSSAL 1966, etc.). Nevertheless, BROUSSAL recognized that great differences occur in dependence on various combinations of host numbers as well as host presence or absence (see: below in *Diaeretiella rapae*).

(a) Different host densities. When a single host was present for the whole lifetime of a parasite, 68.9 eggs were laid per ♀. This was an apparent reduction of the total fecundity (Fig. 237).

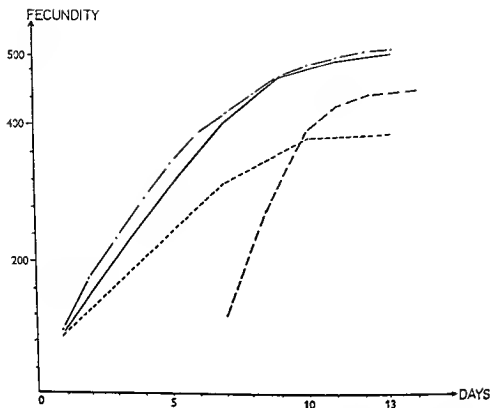


Fig. 238. Fecundity of *Diaeretiella rapae* in relation to presence and absence of host. Host: *Brevicoryne brassicae*. (BROUSSAL, 1966). — normal evolution, —.—.— host present every second day, ---- host present every third day, - - - - host present from 7th day.

When a single host was present during the first 6 days and later 5 hosts were present for the rest of a parasite life, 457.5 eggs per ♀ were laid.

When 5 hosts were present during the first 6 days, and a single host present for the rest of a parasite's life, 429.1 eggs were laid per ♀.

It is apparent how the host density can influence parasite fecundity.

(b) Host presence or absence. Three variations of experiments were made (Fig. 238).

When a host was absent during the first 6 days of ♀ life, 442.5 eggs were produced per ♀. With respect to the fecundity where 5 hosts were present, there was a decrease in the number of eggs, i.e. 63.7 eggs only being laid (12%).

When a host was present every other day, 497 eggs were produced per ♀, the decrease being negligible (0.7 eggs).

When a host was present every third day, there were 383.2 eggs produced per ♀, the decrease being 123 eggs, i.e. 24%.

It is clear that the fecundity of the parasite is reduced in the first and third experiment. In the second case, the absence of host for one day was compensated in the following day as to parasite fecundity.

(c) Principles. First, it is necessary to stress the difference between potential and realized fecundity. The potential fecundity is inherent, the eggs are produced with no dependence on host density. Host density has an influence on the realized fecundity of the parasite. A larger number of hosts causes an increase in the number of laid

eggs up to a certain level per day, which is determined by the number of mature eggs in the ovaries. The age of the ♀ is important in case there is a lack of host for a long period, the presence of a host is not of great value for an old ♀, whose fecundity is reduced by age. All these influences are overruled by the influence of temperature.

9. Temperature defines the lower and upper limit of the rate of egg production. Below a lower limit, the rate of egg production is virtually zero. If temperature increases, the rate of egg production increases up to a maximum and then decreases at still higher temperatures until the upper limit is reached, when the rate again becomes zero (ANDREWARTHA & BIRCH, 1954). This general rule may be illustrated by two examples of the aphidiid group: STARY (1964) studied the influence of temperature on the realized fecundity of *Aphidius megourae*. In fluctuating low temperatures averaging 10–14°C the average number of parasitized aphids was 20 aphids per ♀ parasite, with a minimum of 5 and maximum of 51, while the higher temperature averaging 18–24°C showed the average number of 115 parasitized aphids per ♀, with a minimum of 5 and maximum of 229 aphids. Similar results were obtained by MESSENGER & FORCE (1963) in *Praon exoletum*: at temperatures averaging 12.5°C the average number of eggs per ♀ was 162, while under temperatures averaging 21°C the number increased up to 300 eggs per ♀.

10. Photoperiod. Fecundity is proportional to the rate of photoperiod. Theoretically, if the photoperiod increases, the possibility of host and parasite meeting increases simultaneously. Thus, maximal fecundity has to be at the longest (24 hours) and the minimum fecundity at the shortest photoperiod (FLANDERS). Nevertheless, BROUSSAL's (1966) experiments disclosed that the fecundity of *Diaeretiella rapae* is proportional to the increase of photoperiod, but the increase of fecundity reaches a certain level, which is determined by potential fecundity above which it cannot be increased even if the period were 24 hours. To show this in detail, some results of BROUSSAL must be mentioned (Table 4): *D. rapae* has maximal fecundity at 14 hours photoperiod (500 eggs). The fecundity decreases when the photoperiod is under this optimum (298.1 eggs at 11 hours). Nevertheless, the fecundity does not change substantially over this optimum, at 16 and 24 hours, respectively.

A different photoperiod is responsible also for differences obtained when rearing early spring and aestival generations of *D. rapae* at 11 hours and 14 hours photoperiod conditions (Table 4). MESSENGER (1964) also found that photoperiod influences the production of eggs in *Praon exoletum* in that the ♀♀ tend to lay more eggs when illuminated than they do in the dark, hence, more eggs are laid during long days than in the shorter ones.

11. Season. BROUSSAL (1966) ascertained apparent differences occurring in the fecundity of an early spring generation of *Diaeretiella rapae* that emerged from hibernating mummies, and the aestival generations. The differences were typical for each of the generations mentioned, disregarding whether the ♀♀ were mated or virgin (Table 4). Moreover, the early spring generation lay only one series of eggs that mature during the pupal stage up to the emergence of the adult; no oogenesis occurs in the adult stage in this generation. On the other hand, oogenesis occurs during the whole adult life of the aestival generation, also during the period when the pupal portion of eggs was deposited (BROUSSAL 1961).

Detailed research of fecundity of a species clearly shows that the action of the separate factors is complex. For example, in *D. rapae* we can see the influence of a parasite ♀'s age, mating, host species preference, host densities, temperature, photoperiod and seasonal period; only the research of separate factors under given constant conditions can show their true relations. The factors are also not equal as to their importance.

Generation	Mated x virgin	Photoperiod in hours				
		♀♀	11	14	16	24
First	Mated		179.2	260.4	263.2	262.5
	Virgin		94.4	118.8	115.2	122.8
	Difference		84.8	141.6	148	139.7
Aestival	Mated		298.1	508.4	509	499.6
	Virgin		178	281.8	271	277.8
	Difference		120.1	226.6	238	221.8

Table 4. Fecundity of *Diaeretiella rapae* ♀♀ in dependence on generation, mating and photoperiod. 1. First generation—emerged from hibernating prepupae in spring, 2. Aestival generation. Conditions: + 20°C, 80% R.H. (compiled from BROUSSAL, 1966).

— NUMBER OF GENERATIONS PER YEAR. Conditions of environment determine also the fecundity of the parasites with respect to the number of generations per year. Principally, climatic conditions of a given zone are the primary factor; consequently, the number of generations may vary even at the same plot or area in different years. Moreover, the separate generations are not strictly separated from each other but they overlap. TREMBLAY (1964) recognized 15–16 generations of *Lysiphlebus fabarum* per year in Italy; HAFEZ (1961) ascertained 6 to 11 generations of *Diaeretiella rapae* in 1959, and from 5 to 11 in 1960, in the Netherlands. The number of generations may be also influenced by the diapause.

— BIOLOGICAL CONTROL. The changes in parasite reproductive capacity caused by a different photoperiod seem to be important also in parasite introduction, when the parasite species are introduced from a temperate zone to the tropics, etc. Theoretically, a shorter day in the tropics might also cause decrease of parasite fecundity when compared with its native home in a temperate zone.

The knowledge of factors influencing reproductive capacity of the parasites, of the temperature and photoperiod namely, enables the controlling of mass-rearing conditions at an optimum level. Similarly, density relations must be also taken into consideration.

The knowledge of the influences of temperature on parasite fecundity influences also the rate of cold storage of parasites.

Host density in a given area of release have to be taken into account when the release numbers of an introduced species are prepared.

REFERENCES. 10, 21–3, 129, 153–8, 211, 294, 368, 482–3, 497, 586, 655–7, 666, 679, 681, 753, 756–7, 915–6, 997, 1003, 1005, 1019–22, 1023, 1062, 1111, 1121, 1125, 1231, 1238, 1254, 1271, 1285, 1295, 1299, 1304–5, 1319.

Rate of Development

Rate of development is an important part of the biology of parasites. The corresponding records may help us to separate various populations, recognize some of the factors that influence parasite distribution, interspecific relations, etc. Most of the records that can be found in the literature include only rather general data as to the

rate of development of various parasite species. (GRIOT 1944, *Lysaphidius platensis*; MILLAN 1956, *L. platensis*; SCHLINGER, HAGEN, V.D. BOSCH 1960, *Trioxys pallidus*, SEDLAG, 1964, *Diaeretiella rapae*; SHARMA 1965, *Aphidius transcaspicus*; SKRIPTSHINSKY 1930, *A. avenae*, *Ephedrus plagiator*; SUBBA RAO & SHARMA 1962, *Trioxys indicus*, etc.). Some records show the difference in rate of development due to different periods of the season (ESSIG 1911-12, *Lysiphlebus testaceipes*; BODENHEIMER & NEUMARK 1955, *Pauesia* sp.). Other records mention the difference in developmental rates of the host and parasite with respect to parasite effectiveness (SEDLAG 1959). Nevertheless, we have relatively very few really detailed studies on the rate of development of parasite species (WIACKOWSKI 1960; FORCE & MESSENGER 1965, etc.).

-FACTORS. 1. Temperature and relative humidity. Distribution of a parasite species is basically determined by two main factors, by favourable abiotic and biotic conditions; the historical aspect is necessary as well, but it is omitted here. (see: distribution). As to the first factor, which falls in this paragraph, it is apparent that a parasite species occurs in such places which are characterized by a certain range of temperature. The suitability of these conditions exhibits a number of degrees. The presence of a host is not necessary for the life of parasite adults, but it is necessary for the development and further occurrence of a parasite in a given plot. Nevertheless, as host and parasite are two different organisms, they may need various conditions of the environment. For this reason, their distribution may be different to almost equal (see: distribution). A strictly specialized parasite species is restricted to the host distribution range or at least partially, while widely specialized species may exhibit wider distribution, etc. In every case, the natural requirements of a species are very important when the influence of temperature and relative humidity on a parasite species is studied.

Our work with the material of parasites usually consists of the three groups of data:

(a.) Field observations. In the field, we can establish the general kind of habitat in which a species occurs, whether it prefers colder or warmer places, etc., Similarly, the period of the season which it prefers is important. Field observations, too, show such phenomena as diapause, hibernation, etc., which are the basic points for later laboratory studies. Microclimate conditions are also significant; for example, a microclimate inside curled leaves or inside a gall differs significantly from that of the open environment.

(b.) Records on weather enable us to establish the general data as to temperature, relative humidity, photoperiod during the occurrence period of the parasite.

(c.) Laboratory observations. In the laboratory, we can recognize exact data on the influence of various constant and fluctuating temperatures and relative humidities, photoperiod, etc. Laboratory conditions give us the possibility of separating the influence of various factors, to distinguish the responses and peculiarities of separate parasite developmental stages, etc.

Evaluation of laboratory observations enable us to understand, at least partially, the conditions that are required by a species in nature. Natural conditions must be kept as a criterion of laboratory conditions and vice versa. For example, records on parasites of *Therioaphis trifolii* obtained in the field were later compared with those obtained in the laboratory, and results were used in the evaluation of the occurrence and spread of introduced parasites in the new environments (V.D. BOSCH et al., 1964, FORCE & MESSENGER 1965).

(d.) Sensitivity of developmental stages. There is a basic difference between separate developmental stages of parasites with respect to the influence of temperature and R.H. The aphidiids are typical parasitoids and thus means that they spend a part of

their life as free living insects, and the other part as parasites. It is clearly apparent that during the parasitic phase of their life the influence of abiotic factors is determined through the host's requirements on such conditions, while the free life of adults means a direct influence.

A parasite egg can be influenced in two phases of its development: first, it may be influenced in the ♀'s reproductive system, either being immature or mature, fertilized or unfertilized; further, when an egg is laid, it is influenced through the requirements on temperature and R.H. of the host. An egg might survive quite well when being in a host, but it would be destroyed when the ♀ is killed by the same conditions of temperature and R.H. than the host is able to support. Further, unfavourable conditions can also cause an egg not to be laid at all when high temperatures arrest the oviposition in parasite ♀♀ (see: oviposition).

The larval development of a parasite is characterized by the presence inside a host aphid. Consequently, all larval instars of a parasite are influenced through the host's response to conditions of the environment. There may be some difference in the last instar larva as it kills the aphid and is then influenced by the environmental conditions through the aphid skin or cocoon spun.

Prepupa and pupa, similarly as the last instar larva in its final period, are characterized by their occurrence inside a mummified aphid or a separate cocoon. Differences between the two kinds of pupation and the influence of environmental conditions were first recognized by DUNN (1949), who found *Aphidius* species to emerge from the cocoons, while *Praon* species failed to hatch under the same conditions. Thus, however, could be due to specific requirements of both the species to such conditions. Generally, although the *Praon* type of pupation is less common in the aphidids, the species of this type are distributed from temperate to tropical zones similarly to other aphidid species.

The adult stage is the only stage which is influenced directly by various conditions of temperature and R.H.

The various effects of environmental conditions on parasite stages when being free or present inside a host enable a practical conclusion that the parasite requirements on the conditions during the larval development are determined basically by the host: prepupal and pupal stage has a special position, while free living adults are characterized by the true response of a parasite to the conditions of temperature and R.H. As the adult stage is just the stage which is basic as to the parasite survival and occurrence in a given environment, it is obvious that successful development of a parasitized aphid under certain conditions does not simultaneously mean that a parasite species may occur in these conditions as well. These situations are known to occur in praxis, where the adult inability to survive high temperature conditions restricts the parasite occurrence to cooler environments, although the host occurs in both the environments mentioned (*Aphidius smithi* and *Acyrtosiphon pisum*, *Therioaphis trifolii* and its parasites in California, etc.).

It is usual among the insects that a stage occurs in their development which is most favourable to the influence of a certain temperature and R.H. In aphidids, as at least it seems, larval instars that live inside the aphids are capable of surviving high temperatures which could be fatal to pupae (STARÝ, 1964). In general, the prepupa to pupa stage seems to be very resistant to low temperatures (HAFEZ 1961, STARÝ 1964) as well as to high temperatures (see: FORCE & MESSENGER 1965).

With respect to temperature and R.H. requirements, we can divide parasite development into three phases (1) oviposition - host mummification, (2) mummification - emergence, (3) emergence - adult life. The relative lengths of these phases can vary. For example, while in apparently optimal conditions the period infestation - mumm-

mification and mummification – emergence was the same, with decreasing temperature the first period grew gradually longer than the second one in *Aphidius megourae* (STARÝ 1964).

(e) Tolerance range. Rate of development in a parasite species is restricted by upper and lower temperature limits. According to WIACKOWSKI (1960) the development of *Aphidius smithi* was observed at temperatures between 35 – 90°F, but at and below 35°F and above 90°F no development occurred. At 50°F the development was longest (79 – 96 days). R.H. conditions were also found to be of importance.

Constant conditions enable us to ascertain the detailed response of a parasite species to a given temperature. However, as is known, the conditions that occur in nature are fluctuating, they could include also extreme temperatures, which might be harmful to the parasites. WIACKOWSKI (1960) found that *Aphidius smithi* is not resistant to extreme changes in temperature and R.H. conditions in California in summer; in tests kept in natural conditions with a fluctuating temperature (50 – 120°F) and 80 – 100% R.H. no emergence occurred.

It is known (ANDREWARTHA & BIRCH 1954) that exposure to a high temperature exhibits a certain delay in action in that not the stage exposed but the one following dies in consequence; in such a case, the true harmful effect of temperature is not fully apparent. As ascertained by STARÝ (1964) in *Aphidius megourae*, over 34°C the larvae present in parasitized aphids were able to develop but in mummified aphids the parasite died, consequently, we can presume that after the host aphid was killed the high temperature conditions were unfavourable to the last instar larva, but it was still able to spin the cocoon, although the parasite died some time during the next stage and no emergence occurred. In many species, high temperatures induce quiescent states (see: seasonal history) in which the parasite species are able to survive these adverse conditions.

The origin of a parasite species or population highly determines its response to low temperatures. It is known that species from temperate climates often have a stage in the life cycle especially adapted to survive exposure to extreme cold. Such stages are called cold-hardy stages (ANDREWARTHA & BIRCH 1954). All stages of tropical and sub-tropical species can lack a similar adaptation. As observations of many authors (see: seasonal history) show, cold winter conditions are spent in prepupa-pupa stage in a temperate zone. This stage could, therefore, be designated to be cold-hardy. Adult parasites, although known to be capable of surviving rather low temperature conditions, are not able to survive the whole winter, and egg-larval instars depend on the existence of a live aphid and winter is passed in an egg stage in aphids in the temperate zone.

2. Photoperiod. For the time being we have no records on the influence of photoperiod on the rate of development. BROUSSAL (1966) ascertained various differences in parasite longevity, fecundity etc., with respect to photoperiod conditions, but there are no records on the rate of development included.

3. Host and food. Both the larval and imaginal food may have an influence on the rate of development. Unfortunately, we have no detailed records on the rate of development of parasite species in dependence on different species of their hosts.

4. Superparasitism. FORCE & MESSENGER (1965) recognized that in cases of superparasitism in *Praon exoletum* the larva that survives develops somewhat more slowly than larvae of the same age that develop in non-superparasitized aphids. Superparasitism, therefore, means a slower rate of development.

– BIOLOGICAL CONTROL. It is apparent that laboratory studies require as many general field observations as possible. All notes should be included as brief comment in the samples of species that are selected for biological control purposes. These notes can be

rather helpful in further studies; they enable us to understand the occurrence and spread of the parasite in the new environments, etc. Parasites of *Therioaphis trifolii* in California (v. D. BOSCH et al., 1964) can be mentioned as a practical example.

A parasite species must be released in such a stage that it is capable of surviving under the given conditions. Further, the ability of a given stage to survive extreme conditions of temperature and R.H. must be carefully examined as they can represent one of the reasons why a species fails to establish. It is necessary to stress that extreme climatic conditions in nature may occur once in several years. In the laboratory, certain adaptations may gradually be developed in less suitable populations of parasites (acclimatization).

A comparison of developmental rates of several introduced species is also one of the characteristics which help us in classifying the interspecific relations among the parasite species (see: interspecific relations).

The knowledge of the rate of development of the host and the parasite at various periods of the season enables us to establish their number of generations per year, seasonal coincidence of host and parasite, and partially also the effectiveness of the parasite.

— *Rearing*. The ascertainment of optimum temperatures and R.H. conditions for parasite rearing purposes is a necessary part of a biological control program. Optimum rearing conditions for the host and for the parasite can be different. Less favourable conditions can induce a diapause state in the parasite, while host aphid may continue its development (see: DEBACH & SCHLINGER, 1964).

Cold storage. The limit of temperature for parasite cold storage must be well determined so as not to harm the storage material. Similarly, the period for which the material can be stored in various temperatures must be known. Conditions of cold storage are known to possibly unfavourably influence the sexual products of a parasite, although the parasite adults may not be damaged (see: WIAKOWSKI 1960, 1962).

REFERENCES. 10, 98, 128, 130, 301, 332, 419, 428, 482, 497, 516, 653, 762, 965, 1001, 1019-22, 1039, 1062, 1111, 1121, 1125, 1158, 1162, 1231, 1266, 1295, 1299, 1319.

Dispersal

Dispersal is a recurrent local movement within the geographic area of the species (SMITH, 1959). Certain environmental influences such as weather, population densities, man's agency, etc., may cause a temporary lack of a species in certain parts of the distribution area. Because of dispersal, the populations are able to recolonize such areas after the unfavourable changes in the environment cease to occur. Every species has an innate tendency toward dispersal (ANDREWARTHA & BIRCH, 1954). In the history of a species, dispersal is of a common occurrence (SMITH, 1959).

— *MODE OF DISPERSAL*. Aphid parasites disperse in various ways. We can recognize several modes of dispersal in this respect, a parasite population, however, may disperse using all the possibilities mentioned below, as there are certain preferences or restrictions that are determined by the parasite developmental stage, host specificity range, searching behaviour, etc.

In some species, flight of adults may commonly be observed under certain conditions in nature. For example, *Praon abjectum* adults may often be found to fly and disperse over the plants, either ♂♂ searching for hosts or ♀♀ searching for ♂♂. Flight activity is naturally dependent on weather conditions, the adults preferring to run under less favourable weather conditions. Flight seems to be important namely when

the adults disperse over various parts of a large plant such as trees or shrubs, or when they disperse to other plant specimens.

Passive flight seems to occur in cases of parasite adult dispersal over longer distances. In some cases, it seems to exhibit similar features as the passive flight in aphids. For example, passive flight as a mode of parasite dispersal was mentioned by some American authors in the case of *Schizaphis graminum* parasites, i.e. *Lysiphlebus testaceipes*, when the parasites were observed to disperse in masses following the dispersing aphids (SPENCER, 1926) from southern to northern districts.

Running is a common mode of dispersal of parasite adults commonly observed in many species. It is used when searching for the host on a plant. However, certain species such as *Lysiphlebus fabarum* seem to prefer running as the mode of adult dispersal.

Apterous parasitized aphids do not exhibit changes in behaviour in the case there is a lower developmental stage of parasite present in them. In consequence they may disperse over a plant in search for better food sources like the non-parasitized aphids do. They may, too, disperse to other plants in the neighbourhood. However, parasite searching behaviour and influence of parasite on the host play a significant role. In some aphids, the parasitized aphids just before being mummified leave the colony and are found isolated while other aphids do not. This was observed and well documented by e.g. SCHEURER (1964) in some *Cinara*-species, and these observations can be supported by our own. Parasitized aphids, before being mummified, too, may leave the colony and occur in a place where living aphids can hardly be found: for example parasitized *Acyrtosiphon pisum* may commonly be observed on the upper side of older alfalfa leaves, which healthy aphids do not usually frequent. Different dispersal of parasitized aphids over a plant may be also caused by the parasite searching behaviour as mentioned by GEORGE (1957). According to his observations, parasitisation of *Brevicoryne brassicae* by *Diacretiella rapae* in the upper leaves of Brassica plants was found remarkably high, and this was explained by parasite biology: on the upper leaves, colonies of aphids tend to be small and diffuse, the parasite does not make a long search for aphids as they are sufficiently numerous, and therefore a large proportion are parasitized. On the middle and lower leaves, where the aphid colonies are more dense, the parasites tend to restrict oviposition to these individuals at the edge of a colony because the wax and honeydew quickly immobilize them. However, the aphids in large colonies increase at such a rate that the parasites available can attack only a small part of them. In other cases (e.g. *Lysiphlebus fabarum* and *Trioxys angelicae* parasitizing *Aphis fabae*), parasites attack suitable aphids systematically and gradually, and the parasitized aphids remain as other aphids in the colony. Gradually, if heavily infested, a "colony" of mummified aphids may appear. In other cases still, mummified aphids may be observed to be dispersed over the plant, although they originally were present in a colony. The isolation of aphid mummies is either due to the migration of aphids to new leaves, the immobile mummified aphids being left at the original places. Such a case may commonly be observed in *Macrosiphum rosae* parasitized by *Aphidius rosae* on *Rosa* spp. Or the emigration of non-parasitized aphids from the colony, mummified aphids being left behind, may be of a similar result. Example: Aphid mummies found on *Euonymus europaea* leaves after emigration of *Aphis fabae* in spring.

Alate parasitized aphids occur depending on host instar preference by the ♀ parasite. In some parasite species mostly lower instar aphids are preferred and thus aphids are mummified before reaching maturity; in such a case, higher instar aphids are attacked only occasionally, the dispersal of parasites through parasitized alate aphids consequently being rare. Other parasite species prefer higher instar aphids, so that a certain

part of the parasite progeny may disperse via alate parasitized aphids. Example: *Praon abjectum*—*Aphis fabae*. In other cases, alate aphids are exclusively parasitized, because there are either no apterous adults produced (*Drepanosiphon platanoides*—*Dyscritulus planiceps*), or the parasite occurs at a time when alate aphids are prevalent (*Trioxys phyllaphidis*—*Phyllaphis fagi* in C. Europe).

—KINDS OF DISPERSAL. Every species has an innate tendency to disperse (ANDREWARTHA & BIRCH, 1954). Under natural conditions the population of a species disperses to search for hosts and mates, because of unfavourable weather conditions, high population density, etc. Therefore, dispersal occurs in nature irrespective of man.

Under certain conditions man may accidentally or purposely cause the species to disperse. Agriculture, connected with large changes in field environment every year, causes the parasites to occur in certain places (chronic foci) and disperse from there to the neighbouring cultivated areas in which they are directly or indirectly suppressed in a certain part of the season due to agrotechnical activities of man. Large areas of fields are rather extensive places where aphids can find a considerable amount of food, they disperse to the fields in consequence. Naturally, being host organisms, they are soon followed by the appearance of parasites and other natural enemies. Thus agriculture by producing large plots of suitable environment that are primarily un-inhabited by aphids and parasites (spring) gives them a chance to disperse there in certain parts of the season. On the other hand, the tendency of a parasite species to disperse over suitable environments may be purposely used in biological and integrated control of aphid pests: certain uncultivated plots are protected as they are known to represent foci from which the parasites disperse to the cultivated neighbourhood. Similarly, certain plots are left untreated during treatment to preserve the parasites that later disperse to the treated neighbourhood and attack the re-colonized pest aphids or those that survived the treatment. Furthermore, in the introduction of species from abroad, the parasites are released in certain plots and expected to disperse from there to other suitable environments.

—HOST-PARASITE RELATIONS. Although being a relatively well adapted parasite group, the aphidiids exhibit naturally different features as to dispersal than the aphids. Several opinions illustrate these differences:

—Mode of dispersal — Aphids generally are much more powerful in dispersal than parasites. This is apparently due to their dispersal through alate adults. The parasites are slower in dispersal, except perhaps where their developmental stages are transferred via alate parasitized aphids to new environments.

—Progeny — A further advantage of aphids with respect to the parasites is their dispersal as parthenogenetic progeny. This feature enables them to establish and reproduce easily in new environments. The parasites, on the contrary, are mostly biparental species. They must therefore disperse in a certain density that enables the ♂♂ to find and mate the ♀♀, otherwise only ♂ progeny is produced by unfertilized ♀♀ and the population dispersed fails to establish. There are also certain cases of parthenogenetic reproduction known in the parasites, where the ♀ progeny exclusively or mostly is produced by unfertilized ♀♀, but these cases are relatively few. In the latter case, the aphid advantage is somewhat lower.

—Oviposition — The type of oviposition is basically different in both the groups. Generally, the aphids produce progeny that occur near the ♀ and the colony originates. A ♀ parasite must search for suitable hosts in such colonies, therefore, its eggs are dispersed in accordance with the presence of the hosts. The parasites are consequently dispersed in the frame of a given colony, while the aphids form a more or less close single aggregation (secondary dispersal of aphids is not dealt with). On the other hand, one aphid ♀ may begin one or several colonies depending on whether it

crawls over a plant or not; the parasite, on the contrary, mostly attacks various aphid colonies, its dispersion of eggs being consequently relatively greater with respect to a single aphid progeny.

– Quantity – Aphids are known to produce rather a great quantity of progeny including alate specimens that disperse. Although a part of this progeny fails to establish itself for various reasons, the rest is numerous enough to cover extensive areas. The parasites, on the contrary, are less numerous as to the number of dispersing specimens.

– Colonial type of aphid distribution – The basic behaviour of aphids is of the colonial type. Generally, a parthenogenetic ♀ produces nymphs that stay near the ♀ and a colony gradually originates in consequence. There may be various seasonal differences due to senescence of leaves or stems, density of colony, or special shelters may be searched for by the aphids to deposit winter eggs, etc., but the primary colonial type of occurrence remains the same.

The parasites do not exhibit a colonial behaviour, although they are density dependent. Searching behaviour, host instar preference, and oviposition behaviour are the other features that are peculiar to the parasite group.

– Searching ability – Aphids, because of their movements through the alate specimens, are able to find the host plant relatively easily due to the combination of passive and active flight. Large plots of monocultures grown in a cultivated landscape seem to give many aphid species just a suitable possibility to find their host plants without difficulty. The parasites must search for aphids, either individuals or colonies, and this is much more difficult. In many cases, the parasites find the aphids after they have produced a certain amount of progeny and this numerical advantage is later not overtaken by the parasites.

– Rate of development, number of generations – Aphids have a shorter rate of development and produce more generations per year than the parasites. This feature enables them to produce more progeny that may disperse as well.

– Seasonal history – Host-parasite relationship determines also the seasonal history of aphids and their parasites. The parasites, if they have to find their hosts, must occur somewhat later in the season than their hosts. For this reason, a shorter or longer interval occurs between the appearance of aphids and their parasites in spring (temperate zone). This, and other features such as rate of development, etc., enable the aphids to disperse earlier than their parasites.

– Induction of dispersal – This is also different in aphids and in parasites. In aphids, dispersal is usually induced either by host plant conditions or by population density in a colony. The parasite dispersal is induced by the conditions that occur in the host population as well as by their own population density. The parasites are basically density-dependent.

– Environment – Aphid and parasite dispersal is also very influenced by the environment. In certain environments, such as cultivated fields, some aphid species can disperse easily, while such environments are most unsuitable for parasite dispersal (absence of foci, mode of dispersal, unstable character of the community, etc.).

– Habitat dependence – As we have shown in various parts of this paper the parasites are basically habitat-dependent, i.e. they are to be found in certain kinds of habitat, they never alternate kinds of habitats. Some aphids (heteroecious species in the temperate zone) alternate obligatorily hosts together with habitat alternation, connected with dispersal as well. The parasites do not follow these heteroecious species to the new environments but they are adapted in some way to survive the period of aphid absence in a given type of habitat, i.e. either by a wider host specificity range or by developing quiescent states. Therefore, parasites disperse—following their host aphids

or searching for other hosts—in the frame of a given type of habitat, they never follow their hosts to another kind of habitat (forest, steppe, etc.). As a proof of this statement the occurrence of different parasite complexes in different habitats of the temperate zone may be mentioned; were the parasites to follow their dioecious hosts there would be no such difference. The above statement must be stressed as there are certain opinions mentioned in literature (MACKAUER, 1961, FRANZ, 1964) that heteroecious aphids transport their specialized internal parasites from one host plant to the next. This opinion is incorrect with respect to heteroecious aphids and their parasites: first, heteroecious aphids do not exhibit strictly specialized parasites, on the contrary, their parasites are widely specialized, or to a lesser degree, they have developed quiescent states as a response to temporary host absence. Secondly, if the parasites are really transferred via parasitized alate aphids to habitats of another kind, they mostly die due to unfavourable conditions of microclimate, otherwise there would be no differentiated parasite complexes attacking heteroecious aphids in different kinds of habitats. Under certain conditions we can find mixed complexes, but this is probably due to habitat peculiarities (see: Seasonal history). Aphid dispersal through migration, therefore, may make the aphids free from parasite attack for a short time—before the parasites are able to find them, but this does not mean that the aphids are free of parasites because of migration. Even in cases of obligatory host alternation this dispersal does not make the aphids free from parasite action as they fall under the influence of another parasite complex. This is true for natural environments, while there can be a somewhat different situation in cultivated fields, where the parasites may be absent and disperse to such plots only gradually from the neighbourhood; nevertheless, also in this case, the parasites are members of a corresponding parasite complex.

– **Microhabitat** – The requirements of host aphids and their parasites as to the microhabitat are not perfectly equal, they may differ to a higher or lower degree. As a result of this, an aphid species may be attacked in a frame of habitats of the same kind by several parasite species, which occur in different microhabitats, moreover, there may be certain gaps and in some microhabitats the aphid is not parasitized at all. The aphid, naturally, disperses disregarding the microhabitat distribution of parasites. If the parasites are dispersed via alate parasitized aphids, they may fall under such microhabitat conditions which they are unable to survive and die in consequence. This was observed in *Therioaphis trifolii* and its parasites, *Praon exoletum* and *Trioxys complanatus* (see: V. D. BOSCH ET AL., 1964, etc.), and in *Acyrtosiphon pisum* and its parasite *Aphidius smithi* (see: V. D. BOSCH ET AL., 1964) in some districts of California. Such a relationship is believed to be quite common among the aphids and parasites.

– **Host specificity** – In specialized parasites, the range of their host specificity forces them to disperse following their host aphids or to develop a special adaptation (quiescent state). Widely specialized parasites, however, may find several hosts in a given habitat or not. In the former case, they do not disperse from a given plot but they attack colonies of other host aphid species present. In the second case mentioned, the parasites naturally disperse to the neighbourhood searching for other host species.

– **Parasitization and aphid dispersal**. Parasite larvae of low instars do not cause any apparent effects as to aphid mobility and consequently neither to their dispersal. Both apterous and alate parasitized aphid nymphs or adults disperse in the same way as the non-parasitized aphids. Higher instar parasite larvae cause gradual sluggishness of the parasitized aphids, such aphids move more and more slowly and apparently disperse less intensively too, in some cases the parasitized aphids leave the colony; such a dispersal, however, is rather short as to distance.

– **Form of the parasitized aphid**. Parasites are known to attack generally all the aphid

forms except the eggs and quiescent nymphs and adults. The further fate of parasites is dependent on the dispersal movements of corresponding aphid forms and influenced by the host instar preference of the parasite ♀. Apterous forms, being sexual or parthenogenetic, exhibit naturally less dispersal as to the distance reached than the alate aphids.

In certain cases, dispersal of parasites can be influenced directly through movements of aphids that are just conditioned by a given form. According to the observations of V. D. BOSCH, SCHLINGER & HAGEN (1962) there was a tendency observed in parasitized *Chromaphis juglandicola* aphids (parasite: *Trioxys pallidus*) to move from the leaves and seek sheltered places on twigs and branches, these movements being due to their searching for oviposition sites for the autumn.

– *Host specificity.* Host specificity of parasites plays an important role in parasite dispersal. Host instar preference of the parasite ♀ seems to play a more important role than the host range.

Parasites that attack aphids in low instars kill them before the aphids reach maturity so that there is no possibility for such parasites to be dispersed through parasitized adult alate aphids. It seems that the greatest part of aphidids belong to this group. Naturally, host instar preference possibility plays also a part so that sometimes other less suitable instars may be attacked and another mode of dispersal is also possible in consequence. However, observations on host specificity of parasites undertaken by various authors (see: Host specificity) clearly show that there is an obvious preference in the parasite ♀♀ developed as to the infestation of various host instars.

Other parasite species prefer the higher aphid instars, so that they kill the aphids only a certain time after they have reached the adult stage. In this case, the parasite larvae of lower instars may be transferred by parasitized alate aphids. In some species such a type of host preference is common whether the aphids are alate or not (*Praon abjectum*, *Pr. exoletum*), however, the greatest percentage of alate nymphs' occurrence in aphid progeny causes also the great percentage of such nymphs to be parasitized and consequently in certain periods of the year the dispersal of the parasite through alate parasitized aphids may be low or prevalent. In certain aphids, such as *Drepanosiphium platanoides* (KENNEDY 1966) alate adults occur exclusively; if the parasites attack higher instar aphids, their dispersal follows via alate parasitized aphids as well (*Dyscritulus planiceps*).

– *Oviposition behaviour.* Oviposition behaviour of parasites causes the various dispersal of eggs inside an aphid colony. Some parasites attack the aphids rather systematically in a colony (*Lysiphlebus fabarum*, etc.), so that we can often find a colony to be almost completely parasitized. The other parasites attack aphids rather unsystematically, the parasitized aphids being found in various places in a colony (*Aphidius ervi*).

Host instar preference and reaction of attacked aphid and corresponding parasite adaptation play also a part. If a ♀ lays its eggs systematically in the case of the presence of suitable host instars, the eggs, i.e. parasitized aphids will be less dispersed than in case the ♀ must search for suitable host instars in a colony. Similarly, if the attacked aphid exhibits rather a strong defensive reaction, the parasite may be stimulated and run away for a distance before attacking another aphid. In some cases, the infestation of an aphid by a parasite may cause the aphids to disperse and crawl from the original place; this was observed by VEVAL (1942) in *Myzus persicae* and its parasite *Aphidius matricariae*, and may be confirmed by various observations of our own made on other aphids and parasites.

– *Host-parasite laboratory ecosystems.* Two influences of parasite dispersal on host-parasite laboratory ecosystems have been distinguished up till now:

WAY (1966) found that in systems containing only *Brevicoryne brassicae* and *Diaere-*

tiella rapae the host was quickly eliminated when the parasite dispersal was prevented, but with dispersing aphids and parasites removed, an oscillating host population was maintained for over 300 days.

PIMENTAL & AL-HAFIDH (1963), dealing with *Diaeretiella rapae* and *Myzus persicae*, found that severe parasite pressure causes the host population to decline and eventually to break up into small colonies. If at this time the environment provides adequate space, colonies tend to remain separated, making the distribution of the host discontinuous and relatively inaccessible for the parasite. The relative inaccessibility of host colonies in space, allows some host colonies to reproduce undisturbed and contribute to the maintenance of the host population before the parasite finds and destroys the colony. Therefore, in laboratory ecosystems, intensive parasite action caused host dispersal. However, this kind of aphid dispersal is different from dispersal of aphids due to migration as is found in nature; here, the aphids primarily tend to disperse, the possible temporary escape from parasite action being only a secondary feature.

- **INDUCTION OF DISPERSAL.** Besides its innate character, dispersal of parasites may be influenced by various density independent and density dependent factors:

- **Weather.** Seasonal occurrence of parasite species is primarily conditioned the same as with plants and aphids, by climatic conditions. Under certain conditions, the adult parasites emerge in spring, produce progeny, and dispersal takes place. Weather conditions, too, may cause the aphid host plant to grow more intensively; in consequence the aphids may emigrate from the plants rather soon, before the parasites were able to reach certain population levels; due to the emigration of aphids in such a period that is unfavourable for parasite density, the dispersal of parasites can be also lower than if aphids stayed for a longer time on a given host plant. Similarly, other weather conditions may cause the parasites to enter quiescent states and consequently they do not then disperse.

- **Human agency.** Certain areas such as many fields, etc., are deeply influenced by agriculture (tillage) in the autumn; various insects, including aphid parasites, disperse to these areas in other periods of the season or in the following year. In leguminous annual crops for example, such as *Vicia faba*, we can easily see, first, the entire lack of aphids and parasites altogether; later, alate *Acyrtosiphon pisum* aphids begin to appear, they reproduce and aphid colonies originate in consequence, and only after these colonies are established the dispersal of parasites may be observed too; both the aphid and parasite disperse mostly from fields of perennial leguminous crops in this case. Under natural conditions, however, we do not find such monocultures; crop fields are a typical association developed by agriculture. Chemical treatments by selective insecticides may seemingly influence the parasite dispersal as well due to decreased density relations favouring the parasite.

- **Host population density.** Low density of host population causes the parasites to disperse and search for other hosts in the neighbourhood. However, searching ability plays also a part, determining the degree of parasite dispersal from a given plot. Species with low searching ability seem to disperse more easily than species with a greater aptitude, i.e. species that are able to find hosts at a very low level in a given plot. Emigration of aphids from a colony forces the parasites emerged to disperse in the neighbourhood and search for other hosts, either of the same or of other species. Similarly, low host aphid population density in cases where the host plant conditions are favourable, means less or almost no alate aphid specimens, there is also less probability for the parasite to disperse via parasitized alate aphids.

- **Parasite population density.** According to WAT (1966), and this opinion seems to be well justified, natural enemies of aphids can also be influenced by the numbers of their own species, i.e. when the local density of the natural enemy population rises

above a critical level there is mutual interference which stimulates some individuals to disperse. Natural dispersal is mentioned as usually occurring when the amount of mutual interference is below that which induces significant cannibalism, the infrequency of multiparasitism in nature being presented as one of the examples. The above mentioned opinion seems really to be true for the case of aphidiid parasites as well. However, according to our opinion, other aspects have too to be mentioned. A low multiparasitism in nature is believed mainly to be due to the cooperation among the parasite species, i.e. due to the lack of perfect ecological homologues; dispersal of separate parasite species to avoid multiparasitism seems to be perhaps a feature of poor cooperation among the parasites in a given system, as in well-balanced natural systems, competition among the species through multiparasitism is prevented through their different seasonal occurrence, host instar preference, etc., and finally, by the occurrence and action of hyperparasites, which reduce the number of a parasite species population to a community-dependent level. In less stable communities, though, there may be competition or even displacement of one species by another one. Naturally, under certain conditions, multiparasitism can also be a density-dependent phenomenon (laboratory ecosystems, etc.).

Superparasitism is believed to be a more useful example. It is well known that superparasitism is relatively rare or low under natural conditions, being common in the laboratory, however. Its rare occurrence in nature can be classified as a result of parasite dispersal possibilities. Naturally, also in this case, hyperparasites can be important in reducing a parasite population to a certain level.

— FOCI. As we have mentioned, foci of parasites are important just as sources from which the parasites disperse in the neighbourhood. Generally, because of our results obtained in the classification of parasites with respect to the habitats, there is no doubt that the parasites disperse from the foci merely in the habitat of a similar type. With respect to the features influencing the parasite dispersal, it is evident that the role of foci will be influenced by the same factors. Density dependence of host and parasite populations seems to be perhaps the most significant. Although this feature is specifically dependent, we can expect that the parasites will disperse from the foci, either chronic or temporary, after having reached a certain population density. A still unsolved problem is whether the widely specialized parasites keep all their host species occurring in the focus as a single population or not. In the case of monospecific foci this problem does not exist. A similar problem is the response of the parasite in the foci to the immigration of aphids to the focus, the latter case being a density independent matter with respect to parasite population present in the focus.

— RAPIDITY OF DISPERSAL. For the time being we have no detailed records as to parasite dispersal. However, dispersal of parasites via alate parasitized aphids may be established from the rapidity of spread of introduced parasites to new territories where their host had occurred earlier.

Praon exoletum (= *palitans*): the rapidity of its spread was rather strikingly demonstrated in the Mojave Desert in California in the autumn of 1956 when it was carried by parasitized alate aphids from the Antelope Valley to the Mojave River Valley, a distance of about 40 miles. Similarly, in the south San Joaquin Valley the same species was observed to spread from a single colonization site over an area of about 700 square miles in the autumn of 1956 (V. D. BOSCH et al., 1959). For similar records see: Spread of parasites.

The rapidity of dispersal depends therefore on the mode of dispersal that is prevalent in a certain species. If low instar aphids are preferred by the ♀♀, the dispersal will probably be very low as almost no alate adult aphids will appear containing parasite larvae.

Generally, it seems that the dispersal of parasites via parasitized alate aphids is the most powerful as to rapidity, though it depends on other factors, such as suitability of microhabitat, etc. The records on passive flight of parasites are rather poor to enable a generalization.

— COOPERATION AMONG NATURAL ENEMIES is the basic interspecific relation, although their mutual influence can also include competition or even displacement. This cooperation of natural enemies with respect to aphid dispersal can be recognized in their complementary action, as most individuals which are not found by one natural enemy will be detected by another (FRANZ, 1964). This feature of host-natural enemy dispersal dependence is evident from the comparison of the mode of dispersal of aphids and that of natural enemies, which include quite a number of various predatory and parasitic groups. The dispersal of aphids, therefore, is soon followed by the dispersal of one or another of its natural enemies. From this point of view, aphids sometimes are not attacked by parasites for various reasons, such as poor dispersal, but they will probably be attacked by other natural enemies owing to their complementary action. This state, of course, is true for stable communities, while this cooperation can be less apparent in unstable environments. The situation is quite different in the case of introduced pest aphids, which are usually introduced without their natural enemies, or with only a part of their original natural enemy complex. In consequence, various gaps usually appear in aphid limitation by natural enemies in the new environment, and if other factors of the new environment are also favourable, serious outbreaks may also originate. *Therioaphis trifolii* in California can be mentioned as an example (see: SMITH, 1959).

— APHID-ATTENDANCE BY ANTS. Aphid attending ants seem to exhibit two kinds of relations with respect to the dispersal of parasites: Many species of ants are known to transfer aphids over a plant, causing their dispersal. The ant *Lasius fuliginosus* L. for example was observed to transfer young aphids (*Stomaphis quercus*) to upper parts of the tree on suitable branches, where conditions for the aphids are more favourable, resulting also in greater production of honey-dew, this being useful for the ants (GOLDANICIT, 1958). A similar kind of aphid transport by ants was also described by BOENHJEFIMER & SWIRSKI (1957), in cases of certain root aphids. Although there are no records as to the parasites, it seems to be quite possible for the ants to transfer also parasitized aphids that contain low instar parasite larvae.

As we have mentioned in a separate paragraph on parasite — ants relationship, there is a peculiar case known to occur in *Lasius* and *Paralipsis enervis* relationship. The ants mutilate large portions of parasite wings, thereby making the flight of the parasite impossible, simultaneously, they lower the dispersal possibility through flight. This behaviour may perhaps be intentional, as there is a mutual relationship between the ant and parasite mentioned.

— EFFECTIVENESS. Dispersal of parasites generally can have the following consequences: first, the number of dispersing specimens means a lowering of the total population present in a given plot. Second, the parasite can attack the host in other places. Dispersal, being induced by the density of hosts, parasites, and their relations (see: WAY, 1966), is significantly useful with respect to host-parasite relations in time and space. Rapid dispersal and high searching capacity are phenomena of an effective parasite (HAYD, 1960) enabling an early discovery of the hosts, at low densities and in various environments. A number of such examples could be mentioned in addition to those where poor and slow dispersal of parasites makes them poorly effective also. The latter phenomenon of parasites seems to be rather important in unstable environments for instance.

In certain cases, however, dispersal may have also temporary adverse effects as to

parasite effectiveness. An example may be presented here: *Praon exoletum* was found by SCHLINGER & HALL (1960) to exhibit a greater dispersal than the other parasites of *Therioaphis trifolii* in California, as it is dispersed via parasitized alate aphids for considerable distances. This was found to be possibly a good trait for the species at certain times, but at the same time it was a feature limiting the local parasite effectiveness in a given area: in certain areas of California, the alate aphids were produced in great numbers during the summer. These aphids, both non-parasitized and containing low instar parasite larvae, were carried by the strong prevailing winds for a considerable distance. At the same time no aphid or parasite population was brought into the area by the incoming winds, the local effectiveness of the parasite being temporarily interrupted.

— CONTROL. Dispersal of parasites, either indigenous or introduced species, represents an important matter in biological and integrated control programs. In cases of indigenous parasites, it is necessary to have information as to the mode and rapidity of parasite dispersal from uncultivated to cultivated lands, from untreated to treated plots, etc. The rapidity of parasite dispersal has become a very actual question regarding an integrated control program on various crops in unstable environments.

In introduced parasites, before they become members of a given indigenous fauna, a certain interval is known to occur between the introduction of a species and its effect. SELLERS (1953, FRANZ, 1964) have therefore divided the species into two groups: the first group includes species with a slow rate of dispersal, which reach an equilibrium rapidly, but on a small area. The second group includes species with a rapid rate of dispersal, which reach equilibrium of distribution more slowly, but on a larger scale. The zone of an equilibrium of distribution is that area where emigration is equal to immigration.

SMITH (1939), when dealing with insect populations with respect to biological control, has mentioned a spotted distribution to be a characteristic feature of a species under biological control. The host population consists of groups of individuals, which fluctuate in density independently of one another. One group may be eliminated by a parasite, but in the meantime some host individuals will have migrated and established new groups. The parasite must therefore follow its host and so it must be equal to it in power of locomotion. Aphids and their parasites are just a case of the spotted distribution mentioned. However, it seems that these generalized conclusions must be somewhat completed or modified with respect to aphids and their parasites. First, it seems that a complex action of natural enemies has to be dealt with instead of a single parasite; therefore, a parasite need not be equal to the power of aphid locomotion, as there is a complementary action of natural enemies. Second, as we have mentioned, there is a basic difference between the aphids and parasites with respect to habitat alternation. The parasites do not follow their (heteroecious) aphid hosts to habitats of another kind, as they are more habitat dependent and do not exhibit obligatory host alternation as aphids do, different parasite complexes occurring in various kinds of habitats. Instead, various adaptations have developed in the parasites.

The mode of parasite dispersal is important, also in a biological control program, in release methods of parasites namely. Species with a high dispersal are expected to disperse soon over large plots in the new environment, so that the number of their release sites is lower. On the contrary, species with low dispersal must be released in more places to cover the same area as the previously mentioned parasites. Dispersal of introduced parasites of *Therioaphis trifolii*, of *Praon exoletum* and *Trioxys complanatus*, respectively, may be mentioned as an illustrative example (see: v. D. BOSCH et al., 1957, SCHLINGER & HALL, 1961, etc.). *Praon exoletum* is transported mostly via para-

sitized alate aphids, while *Trioxys complanatus* is slower in dispersal because younger aphid instars are preferred by the parasite ♀♀. In consequence, during the summer and autumn of 1956 in the Antelope Valley of California, *Tr. complanatus* spread over an area of about 10 square miles compared with an area of 100 square miles for a similar period of time of spread of *Pr. exoletum*.

REFERENCES. 10, 21-2, 45, 99, 112, 114-6, 121, 125, 126, 128, 129, 147, 173, 216, 279, 301, 317, 385, 425, 450, 482, 502, 515, 535, 562, 594-6, 611, 615, 618, 668, 679, 681, 688-9, 696, 702, 744, 762, 821, 897, 996, 997, 1003, 1005, 1006, 1011, 1026, 1074, 1082, 1099, 1101, 1117, 1125, 1254, 1278, 1313.

Spread

Spread is defined as movements by some portion of a species which results in a major modification of its geographic distribution area (SMITH, 1959). Some authors classify spread as dispersal on the grand scale (ANDREWARTHA & BIRCH, 1954).

As is known, a species is limited in its geographic distribution by the existence of certain barriers that prevent its spread to other areas. Such barriers are generally of two kinds:

— *Physical barriers.* In this group, large areas of water such as oceans, high mountain ranges, deserts, etc., can be included. Naturally, such barriers are not of equal value for all the species. Some species can spread over smaller seas or deserts, others are unable to do so, etc.

— *Biological barriers.* In aphid parasites, the absence of corresponding habitat and host aphid are the commonest barriers of this kind. Again, these barriers are not equal in all species. A strictly specialized parasite is unable to spread outside the distribution area of its host, while widely specialized parasites may do so under certain conditions, as they may find and attack new hosts in the new area. Similarly, strong, interspecific competition or hyperparasites may also be included in this group.

The barriers may exhibit various relations as to their mutual significance. Sometimes, a species is able to bridge a physical barrier, but the lack of hosts, etc., prevents its occurrence in the new environment. In other cases, a species may occur in another area due to favourable conditions both as to host and habitat, but it is unable to bridge a barrier of a physical kind.

Spread is mentioned as occurring very rarely in the history of species (SMITH, 1959) under natural conditions.

— *Spread and dispersal.* From the definitions of spread and dispersal it is evident that the main difference is whether these movements are within or outside a geographic distribution area of a species. Therefore, spread to a new area is followed by dispersal in this area, i.e. by dispersive movements within the new larger distribution area. The reason for this brief discussion is to stress the fact that the dispersive movements of newly introduced species must be classified as spread, while further movements in newly inhabited territories are merely dispersal. The spread and dispersal of introduced parasites of *Therioaphis trifolii* and *Acyrtosiphon pisum* in N. America can be mentioned as examples. However, sometimes it might be difficult to recognize the difference due to rapid dispersive movements, poor state of faunistic research, etc.

— *MODE OF SPREAD.* Mode of spread is basically identical to that of parasitic dispersal, although it occurs outside the distribution area of a species.

— *Passive flight of adults.* By repeated windstreams in the same direction the adult

aphid parasites can be transferred to the same places as the aphids. This might be a case of parasite occurrence in certain islands not too far from a continent. Naturally the corresponding host aphid must spread earlier than the parasite, or its distribution area must be larger than that of the parasite, etc.

— *Alate parasitized aphids.* The mode of spread is generally similar to that previously mentioned. Today we can hardly decide which of them was followed as usually a certain number of parasitized alate aphids may be commonly found among the aphids mummified by various parasite species, although they prefer to attack low instar aphid nymphs (see: Host specificity).

— *Apterous parasitized aphids.* This mode of spread seems to be due to man's agency exclusively, while under natural conditions it seems to be restricted to dispersive movements only. The transport of vegetables and other agricultural crops, in earlier times for example when young seedlings were transported to other countries with no quarantine measures, is probably responsible for the spread over the whole world of some parasite species (*Diaeretiella rapae*, etc.).

Logically, we have to put here also all the activities connected with parasite shipment for biological control purposes, as they also represent a mode of parasite spread (see: Biological control).

— **KINDS OF SPREAD.** Certain traces of a natural spread of separate parasite species or complexes may be seen when studying the development of separate faunas connected with various floristic zones. Historical changes in climate caused various floristic associations to move to other areas, the parasite species therefore spreading in a similar way (see: Geographic distribution). Otherwise, for the statement whether a species is in spread or not, it is essential to have a good faunistic knowledge of many territories and this is still not the case of our period as to aphid parasites. It seems perhaps, that *Lysiphlebus testaceipes* might be mentioned (N. America—C. America and West Indies—S. America).

Today's distribution of various pest species over the world can be classified as being mostly accidental due to man's agency in transferring various crops from one country to another. Several parasite species may be recognized as spreading in a similar way. We know some precise cases of such a spread, e.g., of a *Aphidius matricariae* strain in California, the latter being restricted to greenhouses and their environment only (see: SCHLINGER & MACKAUER, 1963). For many years, various parasite species were transferred purposely, from one country to another to control aphid pests. In this way the spread of some species occurred in consequence, their distribution area being purposely disjuncted by man. In recent years, we can well observe several such cases; the spread of introduced parasites of *Therioaphis trifolii* and of *Acyrtosiphon pisum* in California is best known. The disjunction of a parasite area due to biological control purposes is mostly due to their role in the control of introduced pest aphids; the parasites are their enemies in their native home and are expected to exhibit the same features in the new environments.

— **RAPIDITY OF SPREAD.** Gradual spread seems to be truly natural. Under certain conditions a parasite species or some of its population are favoured by existing conditions and try to cover new territories as their new distribution area.

This spread is seen in some parasite species today too. However, the poor knowledge of the parasite fauna of various territories is the main factor that makes a more detailed research impossible as yet. *Lysiphlebus testaceipes* may be mentioned as a species that spreads in our period. Being perhaps N. American in origin, a steppe species, it is a widely specialized and common parasite in various parts of N. America. Several strains have been recognized up till now. It seems to spread southwards, to S. America via the West Indies and C. America (STARÝ, 1967). Our observations on

the host range of this parasite in Cuba regarding its total host range may be mentioned as a proof.

Gradual spread, although in a disjunctive area of distribution due to a biological control program, has been recently studied by American authors.

Praon exoletum (= *paltaus*): in the autumn of 1956 carried by parasitized alate aphids a distance of about 40 miles (Mojave desert, California). It spread also in the autumn of 1956 over an area of about 700 square miles (S. Joachin Valley) (v. D. BOSCH et al., 1959).

Trioxys complanatus (= *utilis*): during the summer and autumn of 1956 spread over an area of about 10 square miles (Antelope Valley, California) (v. D. BOSCH et al., 1959).

The same species spread over 100 square miles in south west Arizona alfalfa growing areas between July and September, 1957.

Trioxys pallidus: during 1959 – 1962 spread approximately over 1,000 square miles in California (v. D. BOSCH, SCHLINGER & HAGEN, 1962).

Aphidius smithi reported to spread a minimum of about 260 miles within six years in N. America (MACKAUER & BISDEE, 1965).

The spread of some parasites, due to their slow dispersive movements, is accelerated through the release of parasite populations in new areas in a given country; these areas would be apparently reached by the introduced parasite populations as well, although it would take a long time (*Trioxys complanatus* in California, see: v. D. BOSCH et al., 1959, SCHLINGER & HAGEN, 1961, *Trioxys pallidus* in Australia and Tasmania, see: WILSON, 1960).

– REQUIREMENTS OF HOST AND PARASITES. We have shown in the paragraph on geographic distribution some possibilities of host and parasite synchronization in geographic distribution. Such possibilities are influenced by several factors, such as historical factors, host specificity range, spread, etc., which are complex in action. The parasite distribution area may be smaller or larger than that of the host (s), but it rarely seems to be equal. The differences in requirements of host and parasite on the environment, due to the above mentioned factors, seem to be the reason. Today, we can again deal only with a given state of affairs, having almost no possibility of making comparisons, as our knowledge of the group is very poor in many ways. Historical plant geography, aphidology, and research of parasite complexes will perhaps be most helpful to show at least some traces.

However, we see that the spread of *Aphis spiraeicola* from N. America to S. America seems to be a matter of our recent period, while *Lysiphlebus testaceipes* was quicker in this case, being more widely distributed to the south than the aphid. This is due probably to the wide host specificity range of this parasite, *A. spiraeicola* being its host only in some parts of its distribution area, some populations or strains being unable to complete the development in this host (see: Intraspecific categories, etc.). Unfortunately, we have no information as to the different requirements of both these species as to the microhabitat except for Cuba (STARÝ, 1967).

Different requirements of the host, *Therioaphis trifolii*, and its introduced parasites, *Trioxys complanatus* and *Praon exoletum*, have recently been recognized by American authors (see: v. D. BOSCH et al., 1959, SCHLINGER & HALL, 1960, 1961, BARNES 1960, etc.). While *Th. trifolii* spreads very intensively, covering large areas, its parasites are more selective as to the microhabitat, which prevents or enables their spread into various territories: one parasite is better adapted for hot and dry conditions, another prefers milder climatic conditions.

– EFFECTS OF SPREAD. The spread of parasites may mean that a part of a parasite species population falls under the influence of other environments than of the former

distributional area. New hosts may be parasitized, new interspecific relations originate, the climatic conditions may be somewhat different, etc.; all this may gradually result in the development of adapted strains or even geographical races. The behaviour of *Trioxys pallidus*, an introduced parasite into N. America, can be perhaps mentioned as an example (See: HAGEN & SCHLINGER, 1960). Otherwise we have no detailed information as to the effect of spread on a parasite species.

— BIOLOGICAL CONTROL. The use of the spread of a certain introduced parasite species to control a pest in a given area is one of the main ideas of the biological control of aphids, which is also widely put into practice. For this reason, great interest is paid to the mode and kind of parasite spread, its rapidity, and differences in spread of the pest aphid and the parasite in the new environments. Parasite spread can be predicted to a certain extent on the basis of knowledge of conditions which occur in the native country of the parasite introduced. This was the case of introduced parasites of *Therioaphis trifolii* in California (see: V. D. BOSCH et al., 1959). On the other hand, a parasite species sometimes spreads in a different way from what is anticipated. For example, *Aphidius smithi* seems to spread much more northward (see: MACKAUER & BISDEE, 1965) than one would expect because of its Indian origin.

REFERENCES. 10, 45, 123, 125, 126, 128, 129, 216, 502, 702, 1005, 1082, 1130, 1313; and other references mentioned under dispersal, see above.

Seasonal History

LIFE-CYCLE IN APHIDS. The scheme of development of the life-cycle in aphids has been elaborated comparatively recently by SHAPOSHNIKOV (1959), his conclusions being presented in our paper as well. The schematical pictures and detailed descriptions and examples of various types of life-cycles in aphids may be found in extensive aphidological literature.

According to SHAPOSHNIKOV the following points have been dealt with when reviewing the types of life-cycles: (A) The causes of changes of the life-cycles and origin of diapause, (B) aphid life-cycle, (C) diapause, (D) recent stimuli inducing diapause.

I. (A.) The transition of aphid ancestors in time or in space from a tropical to a moderate climate, and corresponding adaptation to more strictly manifested seasonal prevalence of climate.

(B.) Monoecious cycle. All progeny amphigonic and not differentiated (unknown in recent aphids; observed in other Homoptera).

(C.) Origination of winter diapause.

(D.) Origination of photoperiodic reaction. Note: It is not yet known to what degree and if the periodic reaction always has an immediate influence on an insect. For example, in underground-living aphids, not the length of the photoperiod, but the physical-chemical changes caused by its influence in the substrate—food of aphids—, is presumed to be a stimulus to diapause.

II. A. Adaptation to seasonal changes in cycle of the host (woody plant): Maximal utilization of favourable life conditions in spring-summer period.

B. Parthenogenesis, viviparity (in Aphididae) and strict food specificity appear in spring and summer progeny. In connection with these, the differentiation of progeny appears, their specialization being followed by a number of simplifications, basically owing to a reduction of locomotory and sensory organs. There originates the recent normal monoecious cycle. (In many species in the greatest part of aphid groups).

(C.) Winter diapause is preserved.

(D.) Photoperiodic reaction is preserved. In most aphids it is completed by the

"factor of time": aphids are capable of responding to day-length only after a given time period has elapsed from the moment of the fundatrix's emergence.

III. A. The changes in cycles of woody plants during the process of adaptation to arid conditions of moderate climate. The appearance of unfavourable life-conditions of aphids on these plants during the summer period being the sequence.

(B.) (a) There is a complete alternation of hosts (from woody plants usually to grasses), the cycle being normal monoecious (in many species in very many aphid groups).

(b) There originates at first a facultatively, and later an obligatorily dioecious cycle with seasonal host alternation (in many species in many aphid groups).

(c) There originates an interrupted monoecious cycle with partial or complete interruption of development in the summer period (in aphids of the genus *Periphyllus* of the Chaitophorinae).

C. (a) Winter diapause preserved.

(b) Winter diapause preserved.

(c) Winter diapause preserved, the summer diapause appears.

D. (a) Photoperiodic reaction preserved.

(b) Photoperiodic reaction preserved.

(c) Unsatisfactorily known. Apparently, simultaneously with the photoperiodic reaction (autumn), there is an influence of a clearly food stimulus, which is changed by a fixed number of spring progeny (summer). Note: Such cases are mentioned, when a food stimulus, e.g. common deterioration of food conditions, occurs irrespective of the length of the photoperiod.

IV. A. Changes in cycles of woody plants during the process of adaptation to arid conditions of moderate climate. Origin of unfavourable conditions of aphid life on these plants in the summer period being the result.

B. Reduced monoecious cycle originates.

(a) Facultative (in some species of various aphid groups).

(b) Obligatory (in some species of various aphid groups).

C. (a) Winter diapause preserved, summer-winter diapause originates.

(b) Only summer-winter diapause occurs.

D. (a) Unknown. Apparently, photoperiodic reaction is completed and possibly is changed by a clear food stimulus and later by a fixed number of progeny.

(b) Unsatisfactorily known. There is an influence, apparently of a food stimulus, which is, to a higher degree, changed by a fixed number of spring progeny.

V. A. Unfavourable conditions for aphid life on secondary host (woody plant or herb) originate in the summer period.

B. From the usual dioecious cycle a reduced dioecious cycle originates with preservation of spring-summer migration:

(a) Annual

(aa) Facultative (in *Eriosoma lanuginosum*).

(ab) Obligatory (in some Aphidinae).

(b) Biennial (in Adelgidae and Thelaxinae: Hormaphidini).

C. (a) (aa) Winter diapause preserved, summer origination of summer-winter diapause.

(ab) Only summer-winter diapause preserved.

(b) Only summer-winter diapause preserved.

D. (a) (aa) Unknown. Apparently photoperiodic reaction is changed by a clear food stimulus.

(ab) Unsatisfactorily known. Apparently photoperiodic reaction changed by a clear food stimulus, and later by a fixed number of progeny.

VI. A. In arid zones sun humping of grasses-secondary hosts of aphids in summer and renewal of vegetation in autumn and winter

B. Apparently, from a normal dioecious cycle with spring-summer migration a biennial reduced dioecious cycle originates with autumnal migration (*Eriosomatinae*, *Fordini*).

C. Simultaneously with summer-winter diapause on primary host, there originates also a summer diapause on secondary host plant

D. Unknown.

VII. A. Apparently, following the symbiosis with ants, transition of aphids to life on roots of plants in underground.

B. Normal monoecious or dioecious cycle preserved (in many species of the Eriosomatinae, Aphidinae, Lachninae, Anoeciinae).

C. Winter diapause preserved.

D. Unsatisfactorily known. Apparently photoperiodic reaction (indirect) preserved.

VIII. A. Loss of primary, or, more rarely, of secondary host in dioecious aphid species.

B. Gamie progeny and with it connected part of the cycle loses. Only anholocycly occurs. During a certain period however the ability is preserved to re-establish the complete cycle when the lost host appears (in a number of species of the Adelginae, Phylloxerinae, Eriosomatinae, Thelaxinae, Anoeciinae, Aphidinae). There originates secondary differentiation of progeny: appearance of peculiar spring forms, changing the fundatrices, for example in some *Brachycaudus*- and *Adelges*-species.

C. Winter diapause preserved, but it is transferred to other progeny.

D. Unknown. We may presume that photoperiodic reaction is preserved, being direct or indirect.

IX. A. Transition of aphids from moderate climate to tropical climate (or in greenhouse-conditions).

B. Gradual loss of gamie progeny together with a connected part of the cycle. Anholocycly originates. In connection with this the differentiation of progeny disappears (many species in many aphid groups).

C. Every diapause disappears.

D. —

Some notes need to be added due to some comments of various authors on the development of life-cycle in aphids:

MORDVILKO, followed later by SHAPOSHNIKOV, assumed heteroecy to be the final point of life-cycle evolution in aphids. Nevertheless, HILLE RIS LAMBERS (1949, 1950) has shown that heteroecy is not the finality of life-cycle evolution as there are also cases where heteroecy has been lost, the complete cycle now taking place on the original secondary host.

Similarly, the evolution of anholocycly has been discussed by various authors (see: BODENHEIMER & SWIRSKI, 1957). Anholocyclic viviparae were found in principle just as capable of spreading into new areas as the holocyclic forms. The main barriers to the extension of the anholocyclic forms are—apart from the absence of their hosts—the winter cold in the north and the summer drought in the south. The cleavage into strictly holocyclic migrants, facultatively holocyclic migrants and strictly anholocyclic races is kept as a common phenomenon also within the natural area of the holocycle. Anholocycly on the secondary hosts often, perhaps as a rule, has its origin under quite normal conditions, within the centers of the holocyclic areas, independent of major environmental changes. Neither the disappearance of the primary host, nor exsiccation or glaciation are necessary to induce the cleavage of a holocyclic form into obligatory migrants, facultative migrants and holocyclic (on the primary host) or anholocyclic (on the secondary host) monophages.

ADAPTATION OF APHIDS. The gradual occurrence of unfavourable conditions on trees, the primary host plants, during the summer, forces the aphids to change their mode of life, various adaptations developing in consequence (SHAPOSHNIKOV, 1959):

A. Preservation of basic life conditions through migration to other places.

1. Migration in limits of one host specimen or population.

When unfavourable conditions begin to occur on a certain plant, alated forms start to appear—besides numerous apterous forms—to disperse to other parts of the plant

or other specimens of the given host plant (same species). Example: *Aphis pomi*.

2. Migration between hosts of different species.

The migrants appear before the occurrence of unfavourable conditions, almost all the specimens being alated, migration to a host of a different species follows. Example: *Dysaphis* spp.

B. Retardation to interruption of development.

1. Production of peculiar summer forms of apterous fundatrigeniae with lower fecundity. This adaptation is also classified as being useful for the survival of unfavourable conditions on trees as well as on some herbs. The summer forms of apterous fundatrigeniae are characterized by smaller body size, shorter legs, a lesser number of antennal segments, lower fecundity, and by the ability to live in less favourable conditions, for example by the lack of humidity. The following examples may be mentioned: *Aphis gossypii*, *A. idaei*, *A. ruborum*, *Hayhurstiatataricae*, etc. (SIIAPOSHNIKOV, 1959).

2. Interruption of reproduction of adults, and retarding of development of nymphs. *Drepanosiphum platanoides* occurs during summer, sitting on the underside of leaves at regular mutual distances. This spacing is without tactile response of one insect to another. When being disturbed, the response spreads gradually over the colony and the aphids fly off, grouping in the same manner on another leaf after a short while. These adults do not reproduce during this period (DIXON, 1963, KENNEDY, 1966).

Retarding of development of nymphs may be shown in *Pemphigus spirothecae*; in this case, the development of nymphs of second progeny occurring in galls being rather prolonged (SIIAPOSHNIKOV, 1959).

3. Aestival diapause (in instar I nymph). This is a commonly known case of *Periphyllus*-species. Some of them have a facultative diapause—caused by sucking on fully grown leaves—, while no-diapause nymphs may be found to occur on young leaves at the same time (HILLE RIS LAMBERS, 1947). In other cases, obligatory aestival diapause has developed as a consequence of unsuitable food conditions, being recognizable today in the production of strictly diapausing nymphs by apterous as well as alated fundatrigeniae of determined (second) generation, without respect to the environmental conditions (SIIAPOSHNIKOV, 1959).

Viteus vitifolii enters diapause in instar I nymph depending on the water content in the roots of its host plant (LARCHENKO, 1949).

4. Aestival-hibernal diapause (in egg, instar I nymph, or adult fundatrigenia). *Dysaphis*-species with a reduced life-cycle (*D. devector*) may be mentioned as an example. In this case the influence of an unsuitable period (food conditions) cause all or almost all the members of the fourth generation to occur as normal sexuales, the oviparous females then lay eggs that diapause till the spring of the next year.

Acanthohermes quercus is a similar case, except that the sexuales are represented by members of the second generation.

Hamamelistes spinosus. Aestival-hibernal diapause is spent in instar I nymph in this species (SIIAPOSHNIKOV, 1959).

5. Hibernal quiescence. This state may be quite commonly found among the aphids. In the autumn, the oviparous generation produces eggs, which hibernate, the nymphs emerging with the appearance of suitable environmental conditions during the next spring.

SEASONAL HISTORY OF APHIDS. There is no doubt that aphids represent a group of insects which exhibits a great number of different seasonal forms. In some cases they are extremely polymorphous, in other cases they may be even restricted to one reproductive form.

Nevertheless, just because of the scope of this book, we have found it necessary at least to mention the main features of aphid biology in separate climatic zones, this being later used when showing the seasonal dependences of parasites on their aphid hosts.

— *Temperate zone.* The number of species known, peculiarities in biology and other features have shown that the temperate zone is the most suitable zone for the evolution of aphids as a group. This conclusion has been reached independently by various authors (see: SHAPOSHNIKOV, MORDVILKO, BODENHEIMER & SWIRSKI, KENNEDY & STROYAN, etc.). Moderate warmth, moderate rains, wind, and humidity conditions, together with a number of plant species present (grasses, herbs, shrubs, trees) are generally mentioned to represent an optimal environment. Severe winter is mentioned to be favourable for the formation of diapause eggs and/or aphid migration; a mild winter is less favourable and tends to suppress the sexual forms and winter eggs.

Naturally, the ecological optimum is different in separate groups and species of aphids, there being ones preferring steppe, forest-tundra, etc., conditions.

Temperate zone conditions allow the existence of a complete holocycle, both gamic and parthenogenetic forms occur. Moreover, the gamic part of the holocycle is almost entirely restricted today to the moderate type of climate. The various conditions depending on the seasons of the year tend to the development of arrested states in aphid life-cycle.

Besides this main feature of the moderate climate, a certain number of exceptions due to various reasons may be found, too (anholocycle, etc.).

— *Subtropics.* Observations of various authors reached in various parts of the subtropical belt (see: BODENHEIMER & SWIRSKI, 1957, KENNEDY & STROYAN, 1959, etc.) have shown that a subtropical climate results mainly in the very strong suppression of the gamic part of the aphid life-cycle, the aphids reproducing mostly parthenogenetically. It is a common phenomenon known in a number of aphid species in various areas of the subtropics, that the species which is dioecious in the north is anholocyclic in the southern parts of its distribution area—if this reaches the subtropics, a similar suppression of the gamic part of the holocycle occurs in the monoecious aphids as well. Nevertheless, besides clearly anholocyclic species, also species with an anholocyclic development but with a minor gamic cycle, as well as strictly holocyclic species may be found in the subtropics (see: BODENHEIMER & SWIRSKI).

In the subtropics, the aphids are present in an active life state mostly practically throughout the whole year, there being, however, strict seasonal fluctuations due to the different character of the periods of the year, most of the aphids being conspicuous in certain seasons only. Arrested states in development seem to be less common.

— *Tropics.* Humid tropics represent relatively the most stable environment. Nevertheless, as will be shown in the phylogeny chapter, this environment is generally unsuitable for aphids as a group, only some groups having developed in this zone, besides numerous species penetrating to the tropics from northern parts of their distribution area. Due apparently to the stability of conditions, only parthenogenetic reproduction is known to occur in the aphids in the tropics (BODENHEIMER & SWIRSKI, 1957, TAKAHASHI, fcs. MÜLLER, 1966, etc.). Similarly, obligatory migration and host alternation connected with the production of sexual forms is unknown in the tropics. Migration and host alternation is common in aphids that occur in the tropics, nevertheless, this is clearly a facultative type of migration, being a response to the senescence of host plants, high population density, etc.

Generally, the aphids are present in the tropics in an active life state throughout the year, this being apparently due to the evergreen plant communities as well as climatic conditions.

Nevertheless, seasonal fluctuations occur in the tropics, too. The dry and the rainy season of the year have a different influence on aphids. According to V. D. GOOR'S (1917) studies in Java, the general population peak occurs at the beginning of the dry season. The heavy rains of the rainy season and the prolonged drought of the other half of the year are pernicious to aphids. Only in protected locations were they observed to reach their peak at the end of the rainy season.

According to our observations in Cuba (STARÝ, 1967, etc.), the influence of the dry and rainy season of the year is different in different communities. In the evergreen communities, in the tropical rain and cloud forest zone, the influence is not so apparent as there are green plants throughout the year and the aphids may find their hosts continuously. There is, however, another situation in the tropical deciduous forest and in the savanna zone, as the influence of the dry period is severe—the majority of the plants are in a state of rest, so that the aphids find a relatively low number of green plants in various habitats. Nevertheless, there is a certain number of plants that are green and suitable for aphids during the dry season as well, and the aphids may usually be found to reach a high population density just on such plants; in the dry period, too, they are most important as pests due to the growing of some crops in the dry period. Therefore, the aphids are more concentrated then on a certain number of plants, their colonies being rather numerous, outbreaks being common. On the contrary, the rainy season has a different influence on aphids. On the one hand, various green plants may be found practically everywhere, so that the aphids may find suitable host plants in various places and they need not be so concentrated on a certain number of plants only; moreover, the plants grow and senescent rapidly, so that the aphids are forced to emigrate very often and alternate their hosts. On the other hand, heavy rains apparently cause damage to aphid colonies, such as washing down and death of many aphid specimens.

— *Greenhouses.* It would seem that heated greenhouses represent a relatively constant environment, which will hardly be influenced by out-door conditions. Nevertheless, according to our studies, seasonal changes in populations of various aphids that occur in greenhouses in C. Europe (Czechoslovakia) may well be recognized.

The changes mentioned seem to depend clearly on optimum temperature, daylight, R.H., as well as on host plant conditions.

The aphids of tropical origin were observed to be most common in the autumn, when there was a short day period and relatively low temperature conditions (about 15–20°C on the average) and high R.H. At this time, heating had not yet started. The conditions seemed to resemble those of tropical mountain rain forests; *Aphis spiraeicola*, *Tetraneura aurantii*, both species originally introduced from Cuba for experimental purposes, were most numerous, similarly as in early spring, when the day-length and temperature conditions were similar to those mentioned above—due to

to distinguish this aphid from the other greenhouse aphids of tropical origin, which seem to obviously prefer the winter period, the conditions of heated greenhouses.

The other aphid species found or reared in heated greenhouses in C. Europe (Czechoslovakia), such as *Macrosiphum rosae*, *Brevicoryne brassicae*, *Aphis hederæ*, exhibited parthenogenetic reproduction during winter, the conditions being apparently rather suitable for them as well, as they reached a high population in this period.

Generally, according to our studies in C. Europe, aphids were found to be mostly seasonal pests in heated greenhouses, being most common during the winter. The greenhouse environment at this time, apparently, may be close to their ecological optimum as to temperature, humidity, day-length, and host plant conditions, resembling the tropical environment, to which the aphids are mostly originally adapted.

APHIDS AND PARASITES. The seasonal history of aphid parasites of the present day is the result of a long historical evolution of individual groups in a basic dependence on the evolution of environment, i.e. namely on the evolution of floristic zones and aphid hosts.

The main kinds of adaptation of parasites as to their seasonal occurrence seem to be recognizable, being later dealt with in a more detailed way.

1. Adaptation of the parasites to the life-cycle of the host aphids.

They may be classified as an adaptation to the season through the host, either directly or indirectly. This group of adaptation may be subdivided as follows:

(a) Adaptation to the presence of a host throughout the whole season in a given type of habitat. Apparent host/parasite density dependence might seem to be an adaptation of this kind.

(b) Adaptation to the emigration of the host from the habitat.

(ba) Wider host range. This is a common case in the aphidiid parasites.

(bb) Obligatory aestival-hibernal diapause. In this case, the parasites are adapted to the parasitism on certain hosts that possess a certain mode of life in a certain period. As such a certain mode of life occurs only in a certain part of the year, the host spending the rest of the season living in another mode, the parasites survive these periods in seasonal diapause, i.e. they are in an arrested developmental state till the period when the host appears again in the same habitat and lives again in the same mode of life to which the parasites have adapted themselves. In this case, the host range does not allow the parasites to occur continuously during the season and a peculiar adaptation to the periods of host absence has been necessary. Obligatory aestival-hibernal diapause is a phenomenon of close host/parasite synchronization and parasite specialization. Specialized parasites belong to this group, either to a host or to the mode of host life.

(c) Adaptation to the period when the host is present in the given habitat, its development being, however, retarded or interrupted (diapause, quiescence), or when an unsuitable stage occurs to be parasitized.

(ca) Obligatory aestival diapause. In this case, the parasites spend the period when their hosts are in an aestival diapause state during the season by entering a similar state-aestival diapause. Due to the influence of various factors, the diapause state is terminated approximately at the same time when the host begins to prolongate its active life in the usual manner. Aestival diapause in such cases is, therefore, a phenomenon of close host/parasite synchronization in development. This is supported by the fact that strictly specialized parasites exclusively may be included in this group.

(cb) Hibernal quiescence. Cold winter conditions connected with the lack of green plants represent an extremely unsuitable period for aphids; they spend this

period mostly in an egg stage or as nymphs, etc. Hibernial quiescence in the last instar larva, prepupa or pupa stage occurs in the parasites as well as an adaptation to survive the cold winter period.

2. Adaptations of the parasites to seasonal influences.

These adaptations may be classified as responses to the influences primarily of the season, apparently the host's state being omitted by the parasites. In these cases the parasites may enter facultative diapause at the time and during the time when the host is present in the habitat in a suitable stage for infestation, although sometimes in a low population density. This may be sometimes a feature of different temperature-tolerance limits in the parasite and in the host, which is then responsible for the unsatisfactory synchronization of host/parasite occurrence in the given area. Nevertheless, on the other hand, such adaptation enables the parasites to survive a period of unfavourable conditions and then prolongate their occurrence in a given area.

The adaptations of parasites to seasonal influences are known to occur in the following kinds:

(a) Facultative aestival diapause. It is common in areas that exhibit hot and dry conditions (dry subtropics).

(b) Facultative aestival-hibernal diapause. It is known to occur in areas with hot and dry summers; if summer temperatures are sufficiently high, a substantial percentage of parasite population passes into diapause and there may be essentially no resumption of activity until the next spring.

(c) Facultative hibernal diapause. This state is apparently induced by the shorter day and low temperature conditions.

- PARASITES AND MIGRATION OF APHIDS.

- Host specificity of parasites.

1. Host instar preference. As far as it is known, the greatest part of the species of aphidid parasites attack lower instars of their host aphids, the parasitized aphids being killed by the parasite larva before reaching maturity. However, as various factors play a role during parasite oviposition, other instars may be infested as well and for this reason aphids may reach maturity and produce a certain number of progeny in the case that higher instar aphids were attacked by the parasite. In this way, a certain part of parasites may disperse via parasitized alated aphids (*Acyrtosiphon pisum* and *Aphidius ervi*, etc.).

A certain number of parasite species exhibit somewhat different features as to host instar preference. They either attack higher instar aphids as well (*Praon exoletum*), or they directly infest the alated aphid adults (*Dyscritulus planiceps*). In both cases, the parasites disperse via parasitized alated aphids to other districts.

Although no detailed observations have been made up till now, according to our field observations it seems that the mentioned phenomena are in connection with the habitat dependence of parasites. The parasitization of aphids in lower instars might be an adaptation to preserve the species within the limits of a given type of habitat, while the higher host instar preference in parasitization, resulting in possible emigration of the parasite to other districts, might be an adaptation to a wider dispersal of the parasite. It seems peculiar that the latter case, at least as far as it is known, is known to occur in relatively strictly specialized parasite species, which parasitize aphids that exhibit facultative host alternation only. The parasite dispersal via parasitized alated aphid does not mean, therefore, the emigration of the parasite outside the limits of a given type of habitat. This is true both as to the forest (*Drepanosiphum platanoide*s and *Dyscritulus planiceps*, *Phyllaphis fagi* and *Trioxys phyllaphidis*, *Praon flarinode* etc.), and as to the steppe habitats (*Teneaphis trifoli* and *Praon exoletum*). However, as there are sometimes also other parasites known in the aphids

mentioned, the peculiar host instar preference might be a feature of a peculiar mode of interspecific relations as well. In every case, the parasite dispersal via parasitized alated aphids is apparently successful in the limits of a given type of habitat, otherwise (in dioecious aphids) the parasites are apparently unable to survive in habitats of another type in case of being transferred there passively via parasitized alated aphids. Otherwise the forest complexes might occur in the steppe, too, but our observations have clearly shown that there are differentiated and typical complexes of parasites occurring in steppe and in forest type habitats (see: Geographic distribution chapter).

2. Wider host range as adaptation to obligatory migration. The comparison of the host range of parasites of obligatorily migrating aphids (heteroecy) has shown that none of them represent a strictly specialized species. This may be understood as an adaptation to the emigration of the host from a given type of habitat in a certain part of the season. A strictly specialized parasite could not apparently survive such a period of host absence (except for developing an adaptation as an obligatory seasonal diapause, etc., see below), while a wider host range enables the parasite to attack and develop in other host aphids present in the given type of habitat. A number of examples might be mentioned, only some typical ones being presented in more detail: *Trioxys angelicae*, C. Europe. It is a common parasite of various, mostly aphidine aphids, which live in dense colonies in deciduous forest habitats. It attacks both dioecious and monoecious aphid species. After emigration of dioecious species from the given habitat, it attacks the monoecious aphids that have a similar mode of life, etc., which have remained there. Similarly, it attacks the dioecious aphids in the autumn again, when they re-migrate to a given habitat. For this reason, no adaptation such as seasonal diapause has developed in this parasite, the wider host specificity range being seemingly a better adaptation, enabling parasite activity throughout the whole season. *Praon abjectum*, C. Europe, is a similar case. *Ephedrus plagiator* is also a similar case, although somewhat of an intermediary type. Its host range covers—besides the aphids living in dense colonies on leaves, stems, etc.,—also the leaf-curling aphids. It is also a typical inhabitant of deciduous forest habitats. Similarly, after emigration of the dioecious hosts (leaf-curling species, and in dense colonies freely living aphids) it attacks the monoecious aphids present in the given habitat. It may be found, too, all through the season in the given type of deciduous forest habitat, infesting various aphid species that live in undergrowth, on herbs, etc. In the autumn, it may be found again as a parasite of dioecious aphids as well, which remigrate to the deciduous forest habitats to the primary host plants.

All three examples are rather typical and may be supported by observation of the seasonal occurrence and parasitization of various aphids during the season in C. European conditions.

3. Examples. All the mentioned examples of dioecious aphids are from C. Europe. More detailed records (localities, host plants, etc.) may be found in the author's monograph of the European Aphididae (in press).

Abbreviations used: PHP—primary host plants, SHP—secondary host plants, mode of life mentioned after the kind of host plants.

Pemphigidae

Pemphigus spp.: PHP(galls)—*Monoctonus pistaciaecola*, SHP—?

Thecabius sp.: PHP(galls)—*Ephedrus persicae*, SHP—?

Prociphilus fraxini: PHP(galls)—*Ephedrus plagiator*, SHP (roots)—?

Tetraneura ulmi: PHP(galls)—?, SHP (roots)—*Paralipsis eneris*.

Schizoneura ulmi: PHP(galls)—*Aecopraon lepelleyi*, *Ephedrus plagiator*, SHP—?

Schizoneura ulmi: PHP(galls)—*Aecopraon lepelleyi*, *Ephedrus plagiator*, SHP—?

Aphididae

Hyalopterus pruni: PHP and SHP (occur in more or less the same type of habitat) — *Ephedrus plagiator*, *Praon volucre*.

Rhopalosiphum padi: PHP (galls-leaf curling) — *Ephedrus persicae*, *E. plagiator*, *Monoctonus cerasi*, *Praon abjectum*, *Pr. volucre*, *Trioxys angelicae*, SHP — (freely on grasses) — *Aphidius pascuorum*, rarely *Ephedrus plagiator*.

Aphis fabae: PHP (leaf-curling) — *Ephedrus persicae*, *E. plagiator*, *Lysiphlebus ambiguus*, *Praon abjectum*, *Trioxys angelicae*, SHP — (freely living, sometimes leaf curling) — *Lipolexis gracilis*, *Lysiphlebus fabarum*, *Trioxys aeolephae*.

Brachycandus cardui: PHP (leaf curling) — *Ephedrus plagiator*, SHP (roots and freely living) — *Lipolexis gracilis*, *Lysiphlebus fabarum*, *Paralipsis enervis*.

Dysaphis spp.: PHP (leaf curling) — *Ephedrus persicae*, *E. plagiator*, *Monoctonus cerasi*, *Trioxys angelicae*, *Praon volucre*, *Lysiphlebus ambiguus*, SHP (roots and freely living) — *Lysiphlebus fabarum*, *Paralipsis enervis*.

Hyperomyzus lactucae: PHP (leaf curling) — *Ephedrus plagiator*, SHP (freely living) — *Aphidius sonchi*, *Lysiphlebus fabarum*, *Praon volucre*.

— *Geographical dependence*. It is a generally mentioned fact in the aphidological literature that the life-cycle of an aphid species, as well as the migration as a part of this cycle, exhibits certain changes in accordance with the geographical distribution. The occurrence of sexual progeny is restricted to northern areas, while only parthenogenetic progeny may be found in the southern districts (see above). Thus, there may be holocyclic dioecious species in the northern districts of their distribution area, mixed populations appearing in the intermediary districts, and parthenogenetic populations may be found exclusively in the southern districts (*Hyalopterus pruni*, *Aphis spiraeicola*, *Hysteroneura setariae*, etc. may be mentioned as some of the numerous examples). These features of the life-cycle of aphids also mean that obligatory migration, connected with the production of sexual progeny as well, occurs in northern areas, too, while facultative host alternation does not change with geographic distribution, representing a kind of aphid spread, an adaptation to unstable plant conditions, high population density, etc.

The geographic distribution of aphids is obviously connected with a certain type of floristic zone, although the connections may be wider than in the parasites, several zones being covered due to the peculiarities of the life-cycle. The parasites are clearly attached to a certain type of floristic zone and depend on its distribution as well. In case of the lack of a certain zone in the south, the parasites that are attached to such a zone are absent in the south also.

North-south peculiarities in aphid distribution seem to be obvious, nevertheless, some exceptions may be found in some areas, where the Quaternary glaciation has caused deep changes in the flora and eradication of some species in a given area. In such areas, aphids may have spread afterwards northward when following their host plants. However, in case only secondary host plants have spread, the aphids occur today in anholocyclic populations in the north, while being holocyclic dioecious in the southern districts. *Forda*-species in C. Europe may be mentioned, living here on roots of various grasses and being parasitized by *Paralipsis enervis*, a member of the Eurasian Steppes faunistic complex, while they are holocyclic dioecious in the south, having *Pistacia*-species as their primary host (galls — parasite: *Monoctonia pistaciaecola*, Mediterranean faunistic complex), the latter host plant being, however, eradicated in C. Europe through Quaternary glaciation.

In the tropics, only parthenogenetic progeny has been produced by the aphids. The temperature and R.H. conditions appear to cause much more penetration of various aphids in various types of habitats, and the same seems to be true as to the parasites.

note) of aphids has been classified by SHAPOSHNIKOV (1959) as a historically developed adaptation to the survival of unfavourable conditions of the summer period. Such a classification seems to be clearly understandable, and numerous reasons have been mentioned by this author before this definition has been presented.

Nevertheless, migration (host alternation) of aphids is often classified, among other (nutritional) reasons, as an escape from the parasites' (natural enemies) action. Two such opinions may be mentioned: KENNEDY & STROYAN (1959): "The production of winged migrants is a further main cause of local decline and escape from natural enemies". SCHNEIDER (1962): "The production of winged migrants often causes a local decline of populations and therefore escape from wingless stages of natural enemies". - Parasite occurrence in various habitats - We may deal here only with the aphidid parasites, and it is possible that other features may occur in the predators, nevertheless, we shall try to show that the classification of aphid migration as an escape from parasite action is unjustified, the following reasons being given:

As facultative and obligatory host alternation in aphids represents different cases, they will be dealt with here in a separate way. Facultative host alternation (= vagration of BODENHEIMER & SWIRSKI) seems to be a clear case. If such migration occurs, it means the migration in the limits of one host specimen or host species, etc. It occurs within the limits of a given type of habitat, so that the parasite complexes remain the same. The adult aphids—the alate migrants—are usually not attacked by the parasites in a colony, their presence or absence does not seem to be an important matter as to the parasite action; furthermore, they usually are not the only progeny produced, many apterous adults occurring in an aphid colony simultaneously. When the migrant alate aphids give origin to a new colony of aphids in another host plant specimen, they are apparently soon found by the parasites which are present in the environment. There occurs, naturally, a certain period between the new host aphid colony appearance and the parasite attack, however, it does not seem to be important as to the general host-parasite seasonal occurrence.

It seems general that the aphids are attacked on a certain population density level by the parasites. This is obvious as the alate aphid is usually neglected by the parasites, its progeny not being so numerous at first and a new aphid colony is usually founded after reaching a certain number of specimens. This, naturally, is influenced by a number of other factors that obscure this dependence, such as the presence of food, type of community, searching ability of the parasite, etc. Numerous examples of such a kind may be observed in nature—in the Lachnidae, Callaphididae, Chaitophoridae, and other aphids (monoecious, anholocyclic), and their parasites.

If the parasite attacks alate aphids as well, this being a comparatively less common case, the impossibility of preventing a parasite attack by migration of an aphid is just apparent. For example, detailed observations of American authors have clearly shown that *Praon exoletum*, which attacks the alate aphids as well, is soon dispersed in the new localities in the same way as its host aphid, *Therioaphis trifolii*. Similarly, *Drepanosiphum platanoides* is known to be attacked by *Dyscritulus planiceps*, which is dispersed by alate host aphids as well.

Obligatory host alternation is a different case. This type of migration is connected both with the change of host plant species and the change of the type of habitat; furthermore, the mode of life is often changed in addition.

At first, we shall deal with the conditions on a primary host plant. The degree of parasitization (parasite action) does not really seem to play any role: e.g., it is a commonly observed phenomenon in *Aphis fabae*, on its primary host plant, *Euonymus europaea*, in spring (Europe), that the appearance of alate migrants and their emigration is in connection with climate and corresponding influence of the host

mens or species of primary host plants (*Philadelphus*, etc.). Similarly, in laboratory conditions, in aphid colonies with no parasites present, alate aphids may be found under the influence of certain experimental conditions commonly mentioned (see: biological literature on form determination in aphids).

Conditions on secondary host plants. There is no doubt that *Aphis fabae* leaves the forest-type habitat through the emigration to field type habitats. As the parasites are connected with the forest-type habitats, they in fact do not follow the aphid to the field habitats, as we have already mentioned above. Really, one may observe that, for instance, the aphid colonies on sugar beet in C. Europe are not parasitized for a long time, often being very numerous. This and apparently also related cases were obviously the cases that caused the authors to classify the aphid migration as an obligatory one from parasite action. Nevertheless, the following has to be mentioned: it is a well known fact that various aphids can be found in the steppe type habitats in early spring, at first namely on roots and root collars, later, on higher parts of the plants. At this time, *Aphis fabae* is still on *Euonymus* shrubs. However, at this time the various aphids above mentioned may be found parasitized, and this means that such parasites (*Lysiphlebus fabarum*, *Lipolexis gracilis*) occur in steppe habitats before *Aphis fabae* reaches such habitats after emigration from the forest. If *A. fabae* infests various plants and other plants, its colonies may be found to be attacked by parasites in a very low density, the same density-dependence as the other both migrating and non-migrating aphids. But this is the case when the aphid infests various plants on waste places, meadows, verges, etc. The monocultures of sugar beet represent a different case. The whole field in the given area had been ploughed in the autumn of the preceding year and the whole community was destroyed. The new sugar beet field community starts to exist with the appearance of the phytocenosis—namely with the appearance of young seedlings that are just attacked by the *Aphis fabae*. The parasites do not, however, overwinter in such a habitat so that the aphid colonies can be very numerous usually before the parasite activity is observed, beginning usually at the edges of the field—in the neighbourhood of verges, roadways etc., from which habitats the parasites spread. The black bean aphid leaves the sugar beet plants after they become senescent and migrates (facultative migration!) to various other plants such as weeds, etc., here being soon attacked by the very same complex of parasites—i.e. change of habitats occurs simultaneously with such a type of migration. In the autumn, obligatory migration of the aphid from the steppe or field to the forest (on *Euonymus* shrubs) follows; in the latter habitat, the aphid colonies are soon attacked by the same parasite complex as in spring.

In this connection, too, we should try to show the unjustification of TELENGA's (1950) opinion. This author supposed the parasites of dioecious aphids that occur on old crops during the summer to die after the aphids emigrate from the secondary habitats (crops) to the primary ones, this being naturally connected with their further presence in the field habitats for the rest of the season. He stated generally, that when the parasites are still developing, the aphids emigrate, the parasites then emerge and die due to the absence of the hosts in the field. Although TELENGA's point of view is valuable showing the significance of aphid migration for parasites, his conclusions as to the further fate of the parasites after the emigration of aphids must be classified as incorrect, the following being mentioned: first, the emigration of aphids from the given crop (field) is not a matter of one or two days, being dependent on the state of

various plant specimens, temperature conditions, etc. Further, the dioecious aphids-pests of crops are mostly very polyphagous, they may infest various weed plants present in the field, etc., *Aphis fabae* attacking *Chenopodium* and other weed plants in sugar beet fields being mentioned as a representative of numerous examples. The parasites attacking the dioecious aphids of field crops, being not monophagous species, may find other hosts in the field habitat environment; further, they are usually attacked by secondary parasites in a higher or lesser degree, so that their number is not so high in the late summer season, and, lastly, the aphids and parasites are not present for a long time in the field when it is ploughed, so that there are no hibernation sites of the parasites in the field crops just owing to the earlier emigration of aphids and corresponding dispersal of parasites to other field type habitats (verges, roadsides) (for details, see: Foci of parasites).

A number of similar examples might be mentioned. In the case when the primary and secondary host plants are in a similar or the same type of habitat, the obligatory aphid migration seems to equal the facultative migration with respect to the parasite action (see: Foci of parasites).

In addition, we may notice the records mentioned by SHAIPOSHNIKOV (1959), when dealing with obligatory host alternation in aphids as an escape from natural enemy action: *Dysaphis*-species on secondary host plants were observed to be less attacked by natural enemies than on apple, being protected by the ants on grasses, too. These observations are obviously rather detailed, but we have to mention that the *Dysaphis*-species—in connection with obligatory migration—are attacked by two different complexes of parasites during the season, which are connected with the forest and steppe zones. It is possible that the effectiveness of the steppe complex of parasites is lower than that of the forest.

In the tropics, where there is a lack of obligatory host alternation, although the latter may be found in a species in northern districts of its distribution area, the aphids exhibit only facultative host alternation; similarly, it seems there are also no differentiated parasite complexes in different types of habitats, a species of aphid being attacked by a parasite complex during the whole season.

Therefore, neither facultative nor obligatory host alternation of aphids seem to represent an escape from parasite action.

- *Aphid-vectors*. The important role of migrant alated aphids in the spread of virus diseases of plants is well known. With respect to the possible role of parasites, two basic possibilities may be distinguished: first, the case when the aphid-vectors migrate and attack a given plant specimen. The parasites are unable to prevent the aphid prick in the plant and the transmission of the disease. Secondly, the parasites may prevent the spread of (a part of) aphids from an infected plant as they usually kill the aphids earlier before they can reach maturity and migrate to other plants and eventually transmit a disease.

- *Biological control*. Migration of aphids as a feature of biology of a pest aphid may have a certain significance in biological control as well.

The habitat dependence of parasites means that the type of migration in an aphid has to be kept in mind when a biological control program is elaborated.

The facultatively host alternating aphids occur in a given type of habitat, so that they have to be controlled by parasites adapted for such a type of habitat; in case of facultative host alternation the aphids do not emigrate from a given type of habitat, and they remain therefore in the area of possible action of a certain parasite complex.

The obligatory migration, on the contrary, means mostly the occurrence of an aphid pest at least in two usually different types of habitats. As the parasites are habitat dependent species, the aphid has to be then controlled by at least two different

ecious aphid species—due namely to their obligatory migration—represents a difficult task than the control of aphids that are monoeccious or anholocyclic exhibit only the facultative type of host alternation.

The spreading possibilities of a newly colonized introduced parasite species represent a problem which is closely dependent on aphid migration as well. As to the kind of parasites, they attack higher instars of their hosts less frequently so that adults may comparatively rarely be found to be mummified. Similarly, the spread of parasites via parasitized alated aphids is comparatively poor. Such typical features are known in some parasites of holocyclic monoeccious or anholocyclic aphids, this feature apparently preventing the spread of parasites to another type of aphid.

The host instar preference of the parasites has two sides, at least from the biological control point of view. On the one hand, the infestation of an aphid pest in lower instars means its mummification before reaching maturity, so that a parasitized aphid neither emigrate to other districts nor produce a certain number of progeny. However, the parasite dispersal via an alate aphid adult is made impossible due to the mentioned reasons. On the other hand, the infestation of an aphid pest in higher instars means that the aphid may reach maturity, although being parasitized, emigrate to other districts and there produce a certain number of progeny. However, it is accompanied by the parasites that disperse simultaneously via parasitized alate aphid adults.

The above mentioned two sides of host instar preference may be widely shown on the example of the biological control of *Therioaphis trifolii* in California, where one of the introduced parasites, *Trioxys complanatus*, attacks lower instar aphids, while the other parasite, *Praon exoletum*, infests higher instar aphids and disperses simultaneously via parasitized alated host aphid (see: SCHLINGER & HALL, 1959, etc., V. D. CH et al., 1964).

Integrated control. Two rather important phenomena seem to have been stressed with respect to integrated control.

Anholocyclic or holocyclic monoeccious aphids occur on the given crop (stable environment) throughout the season, they disperse facultatively to other districts of crops growing. Their dispersal seems to be common under favourable conditions, taking part during the greatest part of the season. *Acyrtosiphon pisum*, *Therioaphis trifolii*, etc., may be mentioned as examples. As the period of their dispersal throughout the season is not restricted to a certain part of the season, it seems there is no reason to control the migrant aphids, but to control the aphid population in a crop area as a whole through strip treatment, timing of treatment, etc. Such control measures are known to be applied in praxis (see references of Californian authors dealing with the mentioned pest aphids). However, it is necessary to stress that the aphids mentioned belong to comparatively strictly specialized aphids.

There is nevertheless another case, when also facultative migrants may be dangerous to crops, i.e. through transmission of virus diseases. *Myzus persicae* is just a typical example, transmitting viruses when facultatively migrating during the season on various secondary host plants, from which the commonly known cases—sugar beet, potatoes, etc.—may be cited. We have to add that this is a case of a widely polyphagous aphid species, being thus different from the above mentioned cases of more strictly specialized aphid species.

Holocyclic dioecious aphids, due to their obligatory host alternation, exhibit one common feature: they have trees and shrubs as their primary host plants, while herbs—to which group the various field crops belong—represent secondary host plants. This means that the aphid emigration starts in dependence on climatic features, which influence the senescence of the primary host plants, etc., and cause the production of alated progeny and emigration of aphids to a field. The crops—annual monocultures—mostly do not include any hibernation sites for the parasites, so that the alated aphids that disperse to the given field give origin to new colonies and the parasites are still absent in such a field at that time. The treatment has to be timed to such a period. Later on, when the parasites appear, the damage caused by sucking is usually done, and the treatment cannot prevent the damage by aphids, and, moreover, it kills the natural enemies (non-selective insecticides). Sugar beet and its infestation by *Aphis fabae* in C. Europe may be mentioned as an example.

— PARASITES — DIAPAUSE AND QUIESCENCE OF APHIDS. As both the terms—diapause and quiescence—have often been misunderstood in various papers on aphid parasites, we have decided to give short definitions of these terms also to prevent misunderstanding.

Quiescence represents an interruption of development that is caused immediately and directly by unfavourable environmental conditions. As soon as these unfavourable conditions do not exist, the quiescent state stops its existence, too, and development continues.

Diapause may be characterized as an interruption of development that does not represent an immediate and direct response of the organism to unfavourable environmental conditions, being dependent on impulses of environment that have influenced the organism in precedent phases of its ontogeny. These phases might occur in optimal zone of ontogeny. The diapause starts to occur in such a period when the environmental conditions are still quite suitable for the development of an organism.

Contrary to quiescence, however, the diapause stops a certain time after the unfavourable conditions cease to exist.

According to the period of the year in which they occur, both quiescence and diapause may be aestival, hibernal or aestival-hibernal. Similarly, in dependence on the developmental stage of the organism which is in a given state, both diapause and quiescence may be larval, imaginal, etc. With respect to their occurrence they may be also obligatory or facultative.

We may distinguish the following main kinds of diapause and quiescence in parasites:

1. Aestival diapause. Obligatory aestival diapause seems to be a comparatively rare case, known in some cases of rather close host/parasite relationships. Facultative aestival diapause, although known in some cases exclusively, seems to be a common phenomenon of parasite biologies in subtropic climate areas.

2. Aestival-hibernal diapause. Obligatory aestival-hibernal diapause is comparatively common, being typical for some groups that are specialized for parasitizing certain hosts in a period of the season when the latter possess a certain mode of life. Facultative aestival-hibernal diapause, although known in some cases only, seems to be also a common feature of parasite biologies in subtropical climate areas.

3. Hibernal diapause. Facultative and obligatory hibernal diapause is known in some cases as an adaptation to the survival of unsuitable winter conditions.

4. Hibernal quiescence. This is probably the most common case of arrested development in the parasites, being most typical for the survival of a cold winter period.

As the basic kinds of resting state have often been misunderstood by various authors, we have found it necessary to re-classify such cases with corresponding

changes in the terms used. In the "Review" the records have been listed in accordance with the years, records on country, host aphid and the kind of resting state being added.

Aphidius alius: 1960, SCHLINGER, California, *Macrosiphum rosae*, seasonal diapause 1960, SCHLINGER & HALL, ditto.

Aphidius avenae: 1930, SKRIPTSCHINSKIY, Ukraine, *Rhopalosiphum padi*? aestival diapause. 1966, STARÝ, S. Italy, *Sitobium* sp., aestival diapause. 1966, STARÝ, ditto.

Aphidius cingulatus: orig. records, STARÝ, Czechoslovakia, *Pterocomma* sp., hibernal quiescence.

Aphidius confusus: 1960, SCHLINGER, California, *Macrosiphum rosae*, *Dactynotus rudbeckiae*, seasonal diapause. 1960, SCHLINGER & HALL, ditto.

Aphidius ervi: 1923, MACGILL, Gr. Britain, *Microlophium cransi*, hibernal quiescence. 1954, FEDOTOVA & RJACHOVSKIY, Ukraine, *Acyrtosiphon pisum*, (in living aphids!), hibernal quiescence.

Aphidius funebris: Orig. record, STARÝ, Czechoslovakia, *Dactynotus* sp., hibernal quiescence.

Aphidius megourae: 1964, STARÝ, Czechoslovakia, hibernal quiescence.

Aphidius nigripes: 1960, SCHLINGER, California, *Macrosiphum rosae*, seasonal diapause. 1960, SCHLINGER & HALL, ditto.

Aphidius pisivorus: 1960, SCHLINGER & HALL, California, *Acyrtosiphon pisum*, seasonal diapause.

Aphidius ribis: 1960, SCHLINGER & HALL, California, *Cryptomyzus ribis*,? seasonal diapause.

Aphidius smithi: 1960, HAGEN & SCHLINGER, California, *Acyrtosiphon pisum*, no diapause. 1960, 1961, WLACKOWSKI, California, *Acyrtosiphon pisum*,? diapause-laboratory, 1965, MACKAUER & BISDEE, Canada, *Acyrtosiphon pisum*,? hibernal quiescence.

Diaeretiella rapae: 1926, SPENCER, U.S.A., *Brevicoryne brassicae*, hibernal quiescence. 1957, GEORGE, Gr. Britain, *Brevicoryne brassicae*, hibernal quiescence. 1960, HAFEZ, Netherlands, *Brevicoryne brassicae*, hibernal quiescence. 1960, SCHLINGER & HALL, California, seasonal—?, aestival diapause. 1964, SEDLAG, Germany, *Brevicoryne brassicae*, hibernal quiescence. 1965, SHANDS, Maine, *Myzus persicae*, perennial occurrence—no aestival diapause, no hibernal quiescence. 1966, PAETZOLD & VATER, Germany, *Brevicoryne brassicae*, hibernal quiescence. 1966, WAY, Gr. Britain, *Brevicoryne brassicae*, hibernal quiescence.

Diaeretus leucopterus: Orig. record, STARÝ, Czechoslovakia, *Protolachnus* sp., hibernal quiescence.

Ephedrus persicae: 1960, SCHLINGER & HALL, California, *Myzus persicae*, seasonal—?, aestival diapause, 1962, STARÝ, Czechoslovakia, various leaf-curling aphids, aestival-hibernal diapause. 1966, STARÝ, Czechoslovakia, various leaf-curling aphids, aestival-hibernal diapause. 1966, STARÝ, N. Italy, *Dysaphis* sp., aestival-hibernal diapause.

Ephedrus plagiator: Orig. record, STARÝ, Czechoslovakia, various aphids, hibernal quiescence.

Lysiphlebus fabarum: 1965, TREMBLAY, Italy, various aphids, hibernal quiescence.

Lysiphlebus testaceipes: 1926, ESSIG, western N. America (U.S.A.), various aphids, hibernal quiescence.

Monoctonia pistaciaecola: 1966, STARÝ, Italy-Sicily, *Pemphigus* sp., aestival-hibernal diapause.

Praesia spp.: orig. record, STARÝ, Czechoslovakia, *Cinara* spp., hibernal quiescence.

Praon abjectum: orig. record, STARÝ, Czechoslovakia, *Aphis fabae*, hibernal quiescence.

Praon bicolor: orig. record, STARÝ, Czechoslovakia, *Protolachnus* sp., hibernal quiescence.

Praon exoletum (= *pallans*): 1957, DAVIS et al., California, *Therioaphis trifolii*, seasonal diapause. 1959, V. D. BOSCH et al., California, *Therioaphis trifolii*, hibernal diapause. 1959, SCHLINGER & HALL, California, *Therioaphis trifolii*, facultative diapause. 1960, SCHLINGER & HALL, California, seasonal diapause. 1964, FORCE & MESSENGER, California,

Therioaphis trifolii, hibernial diapause. 1964, V. D. BOSCH et al., California, aestival-hibernial diapause.

Praon occidentale: 1960, SCHLINGER, California, *Macrosiphum rosae*, seasonal diapause, 1960, SCHLINGER & HALL, ditto.

Praon simulans: 1960, SCHLINGER & HALL, California, *Acyrtosiphon pisum*, seasonal — ? aestival-hibernial diapause.

Praon unicus: 1960, SCHLINGER, California, *Macrosiphum rosae*, seasonal diapause. 1960, SCHLINGER & HALL, California, *Macrosiphum rosae*, *Dactynotus ambrosiae*, seasonal diapause.

Praon volucre: 1963, ROTHSCILD, Gr. Britain, *Hyalopterus pruni*, hibernial quiescence.

Trioxys angelicae: 1963, ROTHSCILD, Gr. Britain, *Aphis pomi*, hibernial quiescence. Orig. record, STARÝ, Czechoslovakia, *Aphis fabae*, hibernial quiescence.

Trioxys complanatus (= *utilis*): 1959, SCHLINGER & HALL, California, *Therioaphis trifolii*, aestival diapause. 1959, V. D. BOSCH et al., California, *Therioaphis trifolii*, ? seasonal diapause, 1959, SCHLINGER & HALL, California, *Therioaphis trifolii*, ? hibernial quiescence. 1960, SCHLINGER & HALL, California, ? seasonal diapause. 1961, SCHLINGER & HALL, California, *Therioaphis trifolii*, facultative aestival diapause, 1964, V. D. BOSCH et al., California, *Therioaphis trifolii*, facultative aestival-hibernial diapause. 1964, FORCE & MESSENGER, California, *Therioaphis trifolii*, hibernial diapause, laboratory.

Trioxys indicus: 1962, SUBBA RAO & SHARMA, India, *Aphis gossypii*, ? aestival diapause.

Trioxys pallidus: 1962, V. D. BOSCH et al., California, *Chromaphis juglandicola*, aestival diapause and aestival quiescence.

Trioxys sp.: 1960, SCHLINGER & HALL, California, *Caviarella* sp., seasonal diapause.

Note: hibernial quiescence is widely common in the greatest part of aphidiid wasps all over the temperate zone at least; it is a common state in which the parasites spend the cold winter period. For this reason no other data on hibernial quiescence have been mentioned above, although many such records (original) are known to the author.

- Adaptation of parasites to host diapause.

- Host specificity - 1. Parasitization of suitable host species, host selection. The diapause state apparently requires a well conditioned developmental stage which could survive such a period. It would seem, therefore, that only a suitable aphid host will be preferred by the parasite ♀♀ the progeny of which enters the diapause.

Unfortunately, the greatest part of the cases of diapause is known in strictly specialized parasites (parasites of *Therioaphis trifolii*, *Chromaphis juglandicola* in California, parasites of *Periphyllus*- and *Drepanosiphum*-aphids in Europe, parasites of *Forda*- and *Pemphigus* species in Europe, the Mediterranean, and C. Asia), this being naturally a typical phenomenon of close host and parasite synchronization as to occurrence. There is only one case—that of *Ephedrus persicae*—which is a specialized parasite of leaf-curling aphids in Europe, covering nevertheless a number of aphid species mostly of the Anuraphidine and Myzine groups, in a lesser degree of other groups as well. According to the comparison of the host species found to be attacked by this parasite in Czechoslovakia (STARÝ, 1962), we have ascertained that both main, alternative and facultative host aphids were occurring as diapause cocoons. This would show that all the hosts attacked by this parasite may be used by the parasite to survive the unsuitable environmental conditions in a diapause state—last instar larva or prepupa—which had fed on such aphids before entering the diapause.

Different results have been obtained by SCHLINGER (1960) when studying the diapause in parasites of *Macrosiphum rosae* in California. He observed that some parasite species entered the diapause when parasitizing *M. rosae*, while non-diapausing if attacking other host aphids. According to his opinion "diapause in this case results from the poor synchronization or lack of adaptability to the aphid on the given host plant." We found the records mentioned to be rather peculiar and apparently isolated when compared with all the records and our own observations on diapause

in aphid parasites altogether. There is no doubt that *M. rosae* is an aphid introduced to the Nearctics, while all the parasites seem to be indigenous species of the N. American fauna. Nevertheless, SCHLINGER's observations need apparently further, more detailed observations; the statement that the poor synchronization of host-parasite development or poor parasite adaptability results in parasite diapause, has to be verified.

2. Parasitization of suitable host instars. According to our observations and checking of literature records it seems that there is no peculiar host instar selection in parasite ♀♀ the progeny of which enters diapause in the last instar larva or prepupa stage. This phenomenon seems to be recognizable from the general principles that influence the host instar preference in the parasites, when the most suitable instar for parasite development is being attacked by the parasite ♀ (see: Host specificity).

The extremely apparent large diapause cocoons of *Ephedrus persicae* (mummified *Dysaphis*-, *Myzus*-species, etc.) seemed to show a significance of certain host instars or certain host progeny. Nevertheless, a detailed examination of the mummified aphids-diapause cocoons of the parasite has shown that they represent last instar nymphs or adults of the fundatrigeniae progeny, while some fundatrices have also been found in certain cases. Besides the morphological characters on the mummies, the great number of mummified aphids-diapause cocoons present in one curled leaf have shown that the mummified aphids must be fundatrigeniae progeny, as the fundatrices would be much less in number. Therefore, no selection of certain progeny of the host seems to occur in the case of *E. persicae*.

Nevertheless, a single exception seems to exist in *Monoctonia pistaciaecola*. The examination of the diapause cocoons has shown that they are of unusually large dimensions; besides, no more than a single such cocoon has been found in a gall of *Peniphigus*-host aphid on *Populus*-leaves. This observation has resulted in our opinion that the fundatrices are apparently the only host progeny which the parasite can attack; it is necessary to note that the species mentioned is a specialized parasite of certain gall-producing aphids, and the fundatrices are the only progeny attackable as they are soon closed inside the growing galls—later, when the gall opens, the alated fundatrigeniae progeny appears and emigrates from the gall and simultaneously from the habitat, thus representing a progeny unsuitable for parasitization. The fundatrices, therefore, seem to be attacked in a higher instar by the parasite ♀, nevertheless, it apparently produces a certain number of nymphs before being killed by the parasite larva, as a certain number of aphid progeny may be found inside such a gall when it is dissected.

— Diapause cocoons — The parasite has to spend a certain time in a diapause state. The duration of a diapause state depends on various factors, nevertheless, both in cases of aestival, hibernal and aestival-hibernal diapause, it is a long termed matter. Naturally, special adaptations have developed in the parasites enabling the best protection of the diapause stages during the duration of this state. As the last instar larva or prepupa are the most suitable stages in which the parasites spend the diapause period, the adaptation may be recognized in the spinning of more or less peculiar diapause cocoons.

The diapause cocoons in cases of apparent obligatory aestival-hibernal diapause, which represents a result of strict adaptation of the parasite to the host life-cycle, are clearly recognizable and there is no doubt about their peculiarity if compared with the usual non-diapause cocoons. Two typical examples may be mentioned:

Ephedrus persicae (C. Europe). Two types of cocoons have been recognized to occur in the species in C. Europe (STARÝ, 1962): (a) Non-diapause cocoons. The mummified aphids have the usual appearance of parasitized-mummified aphid. They are mat, blackish, and smaller in relation to diapause cocoons, the segmentation of the

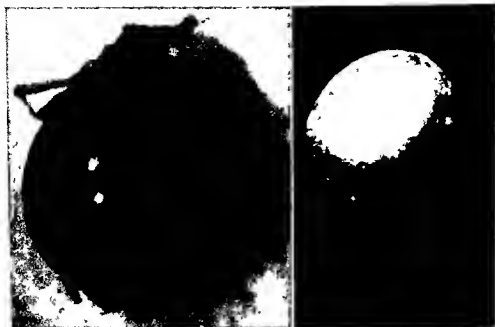


Fig. 239. Diapause cocoon of: left: *Ephedrus persicae*. Aphid: *Dysaphis* sp.; right: *Monoctonia pistaciaecola*. Aphid: *Pemphigus* sp.

aphid skin being easily recognizable. They are strongly fixed to the leaf-surface. (b) Diapause cocoons. The mummified aphids are unusually large, subglobular in shape, shiny, strongly mummified, the segmentation on the host skin being unrecognizable. They are not fixed to the leaf surface. According to the suggestion of Prof. SEDLAC (unpubl. notes) there is not a hole on the underside of the cocoons made by the larva when spinning the cocoon, so that the diapause cocoon is freely fixed among the trichoms of the leaf, etc.; the latter phenomenon seems to be an adaptation to the parasitism on the leaf-curling aphids as the diapause cocoons remain inside the curled leaves, which protect them simultaneously from mechanical injury. No intermediary cocoons have been observed to occur in the species mentioned in Europe (Fig. 239).

Monoctonia pistaciaecola. The diapause cocoons—the mummified fundatrices of the host aphids—are rather large, almost globular in shape, and mat, if compared with the usual normal cocoons of other parasites. Similarly as in *E. persicae*, no hole is cut on the underside of the cocoon to mount the cocoon to the surface of the gall. This seems to be again a result of adaptation to gall-conditions; the gall represents later a defence of the cocoon against mechanical injury. No non-diapause cocoons have been observed to occur in this species (STARÝ, 1966) (Fig. 239).

In cases of apparent obligatory aestival diapause, which represents a strict adaptation to the host life-cycle as well, the diapause cocoons do not seem to be distinguished in any certain way from the non-diapause cocoons produced in other seasons of the year.

Examples: Diapause cocoons of parasites of *Periphyllus*-species (*Trioxyx falcatus*, *Aphidius setiger*, *Praon silvestre*), and parasites of *Drepanosiphum platanoideis* (*Trioxyx cirsii*, *Monoctonus pseudoplatani*, *Dyscritulus planticeps*).

The diapause cocoons in cases of aestival facultative diapause do not seem to exhibit special features, although some differences may exist.

Examples: *Aphidius avenae* (Italy) The mummified *Sitobion*-aphids containing

diapause cocoons of this parasite are remarkably dark brown, being easily distinguishable from the light yellowish brown non-diapause cocoons (STARÝ, 1966).

SCHILLINGER & HALL (1959) reported the occurrence of diapause and non-diapause cocoons in *Praon exoletum*, an introduced parasite of *Therioaphis trifolii* in California. (a) Normal, non-diapause cocoons are white, and clear enough so that the internal parasite is clearly visible through the ventral surface. A brown non-diapause form is also produced but occurs commonly in the autumn of the year. (b) Diapause cocoons, which are brown have several silk extra-layers, so that the developing parasite is not visible through the ventral surface. A white form of diapause cocoons also occurs, but it is found only during the early period of diapause inducement in the autumn of the year. Nevertheless, according to FORCE & MESSENGER (1964) observations made when rearing the parasite under different experimental temperatures, no such classification was found to be useful: the cocoons varied from one category to another, both as to colour and construction. Similar observations on the diapause cocoons have been made by FORCE & MESSENGER in *Trioxys complanatus*, another introduced parasite of *Th. trifolii* in California.

The doubtful value of colour of cocoons for the establishing of the diapause has also been observed by V.D. BOSCH (1962) in *Trioxys pallidus*, an introduced parasite of *Chromaphis juglandicola* in California, the diapause cocoons mostly being light brown in colour, but some were very dark.

Similarly, WIACKOWSKI (1962) has observed the occurrence of (a) light brown and thin, (b) dark brown but thin, (c) dark brown and very thick cocoons, when examining the influence of a combination of 50°F and 10 hours constant light on *Aphidius smithi* in the laboratory.

Summarizing the above mentioned records and opinions on the diapause and non-diapause cocoons we may conclude that in the cases of obligatory aestival-hibernal in diapause, which is in close connection with the host seasonal occurrence, peculiar diapause cocoons are spun by the parasite larvae (*Ephedrus persicae*, *Monoctonus pistaciaecola*). The lack of a hole on the ventral side of the cocoon made by the larva to mount it to the surface seems to be a typical adaptation. The morphological changes recognizable in diapause cocoons might perhaps be an adaptation to parasitism on gall aphids.

In other cases of diapause, the cocoons of diapause and non-diapause state do not seem to be distinguishable as to their morphological characters. The facultative or obligatory diapause, aestival or hibernal, etc., do not seem to play any part. The thicker cocoons, according to laboratory observations of various authors, seem to be a response of a parasite larva to extreme—both low and high—temperatures, as well as the colour of the cocoons.

— Developmental stages — All the literature as well as our own observations agree in recognizing the last instar larva — prepupa to be the stage in which the parasites spend the diapause period. No differences seem to occur between obligatory and facultative, or aestival, hibernal etc., diapause.

This phenomenon appears to be obvious if the characters of other parasite stages are compared with the last instar larva-prepupa stage. Eggs and lower instar larva depend on the living hosts being unsuitable for the diapause state. The adult is mobile, apparently more vulnerable to physical injuries. The last instar larva or prepupa are defended against mechanical injuries by the cocoon and indurated aphid skin, being mostly mounted to the leaf surface or occurring inside the galls.

— Synchronization — Although there can be no doubt about the necessity of seasonal dependence of parasites on their hosts, the cases have to be mentioned and grouped in a certain way:

1. General synchronization of parasite occurrence with the host occurrence (in a given type of habitat). The host occurs for the whole season in a certain kind of habitat (fields), it possesses a certain mode of life. Similarly, the parasites start to appear in a certain period of the season, a host-parasite population system then occurring. This is a common case in aphid parasites. Many cases—permanent or semi-permanent communities—may be mentioned: *Acyrtosiphon pisum* and its parasites in C. Europe, *Brevicoryne brassicae* and its parasites in C. Europe.

The diapause is usually not developed in such parasite species, there usually being only seasonal fluctuations in population densities of both host and parasite. Facultative diapause is known to occur under mentioned conditions only in some introduced parasites of *Therioaphis trifolii* in California, being a response of parasites to unsuitable environmental (climatic) conditions, which are connected simultaneously with the host scarcity. In the dry subtropics, nevertheless, facultative diapause appears to be a common phenomenon—an adaptation of parasites to survival of adverse conditions (hot summer).

2. Synchronization with the appearance of a certain mode of life of the host. In this case, the host—due to the peculiarities in biology—changes its mode of life several times during the season: for example, certain aphid species may be leaf-curling in spring, root feeding in summer, and a freely living species on leaves in the autumn. The parasite—because of its host specificity range—occurs during a period in which the given host possesses the mode of life to which the parasite is specialized. Such a type of occurrence of parasites is made possible by the obligatory seasonal diapause. *Ephedrus persicae* is an inhabitant of deciduous forest habitats in Europe, being a specialized parasite of leaf-curling aphids. Thus, it occurs exclusively during the period of various leaf-curling aphid species occurrence, and it spends the rest of the season, as well as the period of the next year before the leaf curling aphids appear again, in aestival-hibernal diapause state (C. Europe).

3. Synchronization with a certain period of a certain mode of life of the host's appearance. In this case, the host changes its mode of life several times during the season, nevertheless, only a certain part of a certain mode of life is suitable for parasitization. The parasite, due to its host range as well as to the peculiarities in host biology, appears in a certain period, when the mode of the host's life cycle is most suitable for him. The fact has to be stressed that only a part of a certain mode of the life period of the host is suitable for the parasite. Obligatory seasonal diapause seems to determine such a dependence of a parasite on the host occurrence. *Areopraon lepelleyi* is a specialized parasite of gall aphids (*Schizoneura*, etc.). Nevertheless, the parasites do not seem to occur at the time when the forming of the gall starts, and later the complete gall is closed and the parasite, if it were present, would be unable to penetrate inside it through its walls. Therefore, the parasite seems to appear just in the period when the gall begins to open (last stage) to enable the aphid to emigrate, etc. In this period, the parasites invade the gall through the holes, attack the aphids and develop. Although no detailed observations have been made up till now by us (no diapause cocoons ascertained) we may suppose the aestival-hibernal diapause to occur probably in this species as well, otherwise such an exact synchronization of parasite and host would not seem possible. There is another possibility, too, that *A. lepelleyi*—being a parasite of gall and leaf-curling aphids—occurs at first as a parasite of leaf-curling aphids (*Schizoneura ulmi*) and only later it attacks the gall aphid in the open galls (*Sch. lanuginosum*). Nevertheless, due to the biology of all these gall (gall and leaf-curling) aphids, there has to occur aestival-hibernal diapause in the parasite. If the second possibility will be found to be true, the third type of "synchronization" could be classified as a modification of the second type.

4. Synchronization with the occurrence of certain host stage. Usually, and this seems to be the most common case, the parasites are polyvoltine species. As there may be a host instar preferred by the given parasite species found in every aphid colony, no strict synchronization of parasite-host stage is necessary. The fundatrices-parasites relationship seems to include some exceptional cases: Usually, the fundatrices appear earlier than the parasites and only under exceptional climatic conditions they may be found to be parasitized. Example: *Dysaphis* spp. and their parasites. Nevertheless, there exists one rather peculiar case, when the parasite seems to attack just the fundatrix exclusively, spending the period until the fundatrix's appearance the following year in a aestival-hibernal state. *Monoctonia pistaciaecola*. The parasites occur from C. Asia, the Mediterranean, to C. Europe, being inhabitants of forest type habitats. It is a specialized parasite of some gall-aphids (*Forda*, *Pemphigus*). In the material of aphid galls of the mentioned species we have found diapause cocoons of the parasite exclusively, usually a single cocoon in a gall. A later examination has shown that the fundatrices were exclusively parasitized. It seems therefore that the fundatrices—due perhaps to their large size—are the only stage suitable for the infestation by the *Monoctonia* parasite. As the fundatrix lives freely until the gall is formed by the plant, it is suitable for attack, its progeny—the fundatrigeniae—is smaller in size and seems to be unsuitable for the parasite. Later on, the gall is closed and this state lasts until the opening of the gall and the emigration of the aphids. The parasite would be able to search for the aphids not before the last mentioned state of the open gall. To show the factors probably determining the parasitization, the above mentioned may be summarized as follows: (1) The parasite is adapted to some species of gall aphids exclusively; (2) the aphid hosts are dioecious and leave the habitat after the galls are open; (3) they do not cause any galls till the end of the season, although they return to the primary host plants (trees) in the autumn; (4) all forms of aphids are unsuitable for the parasite except the large fundatrices. It seems therefore that the parasite ♀ attacks the fundatrix before the gall is formed, the fundatrix being, however, able to produce a certain number of progeny so that the colony of aphids inside the gall then normally develops. As no other suitable host instar of the given species, nor a similar stage in other hosts in a later period may be found, the parasite spends all the period until the fundatrix's next occurrence in an aestival-hibernal diapause state. The biology of *M. pistaciaecola* will apparently be still more complicated than it seems to be, only relatively superficial field observations being at hand. There may be certain differences with respect to the parasitization of *Forda*-species and *Pemphigus*-species. As to the Fordinae, the following summarizing note of SHAPOSHNIKOV (1962) may be mentioned: "The origin of the Fordinae, similarly as well as that of their hosts, Pistacia-species, is connected with arid areas (DAVATCHI, 1958). The records on biology and ecology of the Fordinae obtained in Israel (WERTHEIM, 1954, 1955) show that the origin of the recent cycle is connected with the arid zone conditions as well. The transfer of the period of aphid migration from summer to autumn, the appearance of arrested state resembling diapause, and the appearance of biennial cycle has to be classified as an adaptation to the year's cycle of their secondary hosts—the cereals. Cereals start growing only after the onset of the autumn rainy season and for this reason, the greatest chance to survive have the aphid migrants which develop the latest. On this base, we may understand the fact, that in all biennial species the galls open much later than in the annual species (*Slavum wertheimae* H.R.L.)." Moreover, the fundatrix of some of the Fordinae species causes the appearance at first of a small gall, the large gall being caused by the appearance of the progeny. In *Pemphigus* species, i.e. in species which are attacked by *Monoctonia* in the temperate zone (C. Europe) where *Forda* aphids (with the exception

of the anholocyclic species) are absent, the situation is different, both as to the cycle and gall formation.

5. Seasonal occurrence, no particular synchronizaton. This may be classified as an extreme and exceptional case in the host-parasite seasonal synchronizaton. In this case, the parasite host range and its biology as a whole enables it to parasitize the mostly on root or root-collar living aphids. To say it more precisely, it may belong to an ant-nest community, being fed by ants. The seasonal history of different aphid species causes that during the whole season some aphid species may be found on roots, either root-collar aphids in spring, or root aphids and root collar aphids in summer and autumn. The parasite, therefore, does not need to be synchronized with any particular host aphid, moreover, it seems to pass winter in hibernation quiescence in an adult stage as a member of the ant-nest community, appearing in spring in the period when the aphids start to appear on the roots or root collars as well. No diapause state is necessary.

- *Adaptations of parasites to host quiescence.* Our field observations carried out on numerous species in C. Europe have shown that parasites spend the hibernation quiescence period in hosts they parasitize in the autumn before entering the quiescent state.

- *Quiescence cocoons* - As it is generally known the aphids mummified in lower temperatures are relatively larger as well as the parasites which emerged if compared with those mummified and emerged in high temperature conditions. Such mummified aphids are generally of a darker colour, too. This phenomenon is true also for the hibernation quiescence cocoons, being apparently influenced by the lower temperature conditions that occur in the autumn.

- *Developmental stages* - The aphids hibernate mostly in an egg stage, remaining in such a stage until spring of the following year. The egg stage is undoubtedly the most advantageous stage in which the aphids can survive the cold winter conditions.

The parasites have adapted in a similar way, surviving winter in a most suitable stage as well. Nevertheless, in this case, it is neither the egg nor lower instar larva stage, which depend on the occurrence of living aphids, nor the adult parasite, which is unable to survive the severe cold conditions of winter, although they are able to survive such conditions for a shorter time. According to SPENCER (1926) the adults of *Diaeteliella rapae* survived temperatures from -12° to $+10^{\circ}\text{C}$, but were unable to overwinter. The last instar larva, prepupa or pupa, which do not depend on the existence of a living aphid, may survive changes of temperature and are protected against a mechanical injury by a cocoon, are the most suitable stages in which the parasites hibernate. Numerous observations of various authors (MACGILL 1923, SPENCER, 1926, ISSIG, 1926, ROTHSCILD, 1963, HAFEZ, 1961, SEDLAG, 1964, etc.) and those of the author (STARÝ, 1964, 1966, etc.) are of the same opinion, i.e. that parasites survive winter inside cocoons.

Certain differences may be found in opinions on the hibernating stage, both last instar larva, prepupa or pupa being mentioned.

Rather interesting observations have recently been published by BROUSSAL (1966). This author made a histological comparison of normal last instar larva, normal prepupa, and hibernating last instar larva of *Diaeteliella rapae*. With respect to the results obtained on the ground of histology he classified the state as pseudo-quiescence, an adaptation to hibernation period. Hibernating last instar larva exhibited the following differences if compared with normal last instar larva: epithel of prepupal type, dehydration of meconium, histolysis of silk glands, the differences with respect to normal prepupa were as follows: structure of alimentary tract similar, dehydration of meconium identical. In hibernating larva the development of

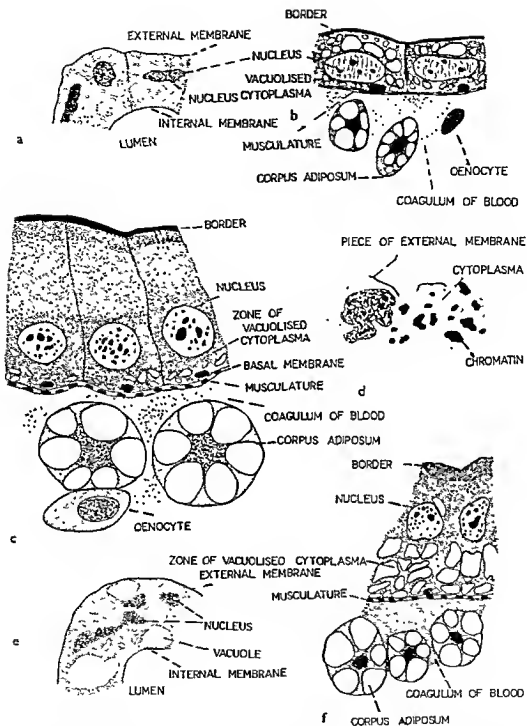


Fig. 240. Histological sections showing differences in structure of intestinal epithelium and silk glands of normal last instar larva, normal prepupa, and hibernating last instar larva of *Diacretella rapae* (redrawn from BROUSSAL, 1966). Structure of intestinal epithelium (a section), b - normal last instar larva, c - prepupa, f - hibernating last instar larva. Silk gland (transversal section), a - normal last instar larva, d - prepupa, e - hibernating last instar larva.

imaginal organs is inhibited, while silk glands, which are a typically larval organ, are degrading and atrophying, being nevertheless present during the whole hibernation period (Fig. 240). BROUSSAL classified the stage mentioned as having a pathological character. He stressed his opinion by observation on the fecundity of first generations and aestival generations of the parasite, of which the spring generation exhibits lower fecundity, there being virgin or mated ♀♀. In our opinion, there can be no doubt about the differences between normal last instar larva, prepupa, and hibernating last instar larva, respectively; the histological proof shown by BROUSSAL is satisfactory enough as well as his observation on the different fecundity of various generations during the season. However, it seems perhaps incorrect to classify the state as exhibiting pathological features: it is highly improbable that the whole group of aphids would adapt itself to survival of hibernation period in the temperate zone in a pathological way. Of course, hard winter conditions may result in lower fecundity of spring generations, etc.

There is probably one exception known to occur among the aphid wasps—*Paralipsis enervis* (STARÝ, 1962, 1966). This species was found to hibernate in an adult stage in an ant-nest. This is undoubtedly the adaptation of the species mentioned as it is a highly specialized parasite of root aphid species attended by ants. This phenomenon—the close parasite-aphid relationship—enables the parasite to hibernate as an adult in the ant-nest community in a similar way as other symphyla and other members of the ant-nest community do.

—Synchronization—The parasites seem to occur in a community until an almost entire lack of aphids in the late autumn or in winter:

In C. Europe, in the late autumn, *Ephedrus plagiator* and *Praon volucre* may be found to attack *Hyalopterus pruni* that occur on reeds and begin to migrate to plum trees (primary host plants). In the same time, the parasites also parasitize the sexuales of various aphid species, that migrate to Rose-shrubs (primary host plant)—*Sitobium*, *Metopolophium*, etc.

Similarly, all the three common parasites of the black bean aphid (*Aphis fabae*) can be found to attack the oviparous ♀♀ that occur in the late autumn on *Euonymus europaea*; numerous parasite cocoons may be found among the aphid eggs laid on the bark of young branches.

In the perennial field communities, two typical cases may be mentioned (C. Europe): *Aphidius ervi*, *Praon dorsale*, parasites of *Acyrthosiphon pisum*, may be found late in the autumn attacking oviparous aphids that lay eggs on alfalfa. *Diactettella rapae* is known to occur actively till the very late autumn and also in winter, attacking *Brevicoryne brassicae* (apparently the tropical, parthenogenetic strain—author's note) on Brassica crops.

There is a basic difference between the seasonal occurrence of aphids and parasites as to the hibernation quiescence quarters.

As has already been mentioned, the parasites occur in a certain type of habitat during the whole season. That means that the parasites also hibernate in the same type of habitat in which they occur throughout the year.

In aphids, there may be a similar seasonal history in holocyclic monoecious or anholocyclic species. Nevertheless, there is a difference in holocyclic dioecious species, that usually change the habitat in accordance with their obligatory migration. In the latter case, nevertheless, the habitat of primary host plant—i.e. the forest type habitat in all cases—is the most important. From this habitat the aphids emigrate in the late spring and re-migrate there in the autumn. Their sexual progeny that occurs on the primary host plants in the autumn and produces the oviparous progeny that lays eggs, is therefore attacked by the same parasite complex as in spring.

The parasites occurring in steppe type habitats may hibernate in holocyclic monocious or anholocyclic aphids, as the dioecious aphid species do not occur in these habitats except for the summer period.

— *Geographic distribution.* The aphids have generally spread over the world in the following two ways: (1) Natural spread, (2) Human agency (accidental introduction with crops, etc.).

The natural spread is mostly gradual so that the parasites usually become adapted, or the parasite area may be even greater than that of the given aphid, the latter case being common in certain widely specialized parasite species.

Strictly different is the case of aphid spread through man's agency. It is usually connected with the overcoming of a certain geographic barrier (ocean). If the aphid finds the new environmental conditions suitable for its occurrence, then under certain circumstances, it may become a serious pest. The latter case is typical for some aphids that are taxonomically and ecologically isolated from indigenous fauna of the given area; in this case the indigenous parasites do not adapt themselves at all or only very slowly: *Therioaphis trifolii* and *Chromaphis juglandicola* in California may be mentioned as examples. Otherwise, if the aphid is taxonomically-ecologically related to the indigenous fauna, the parasites usually soon adapt themselves to a various degree.

As mentioned above, the arrested development is an area-dependent phenomenon. This means that the native parasites occurring in a certain area may or may not possess certain adaptations of this kind, nevertheless, they do not seem to change these features due to the adaptation to parasitism on a newly introduced host species; synchronization of various degree is then the result. On the contrary, a newly introduced parasite species must adapt itself to the new environment, in which it has to occur—adaptation to climatic conditions, new alternative host parasitization, etc.—resulting in either unsuccessful establishment or in its occurrence depending on its ecological optimum, which may be of a somewhat different kind than had been planned by the biological control specialist before the introduction of the parasite was made.

— *Horizontal distribution* — The comparison of separate cases of an arrested development state in the parasites has shown that certain differences may be found in the three basic climatic belts, representing results of adaptation of parasites to the changes and peculiarities of the aphid life-cycle, which exhibits apparent zonal dependence.

1. Temperate zone. Hibernation quiescence is a rather common phenomenon in a number of species, enabling the survival of a cold winter period. Aestival diapause and aestival-hibernal diapause are rare, representing apparent consequences of parasite specificity, which makes the parasite occurrence impossible except during the period when a certain stage or certain kind of mode of host's life may be found.

2. Subtropics. Aestival diapause is very common, enabling the survival of hot summer conditions. Aestival-hibernal diapause occurs too, under similar circumstances as in the temperate zone. In comparison with the temperate zone, seasonal summer diapause seems to be very common in parasites occurring in the subtropics. For example, according to SCHLINGER & HALL'S (1960) observations, diapause has been ascertained in 12 of the total number of 22 parasite species found in California. For comparison, the author has ascertained 8 cases of seasonal diapause of the total number of 105 species found in Czechoslovakia.

3. Tropics. Because of the conditions of climate (photoperiod, temperature and humidity), as well as because of historic conditions, such aphid species are today distributed in the tropics that represent common and widely distributed aphids, besides a less numerous typical tropical aphid fauna. The commonly occurring phenomena have to be stressed in this connection, that the species that are holocyclic

(dioecious) in the northern parts of their distribution area are anholocyclic in the tropics, due clearly to the suitable conditions of climate which is not connected with such strong changes as the cold winter in the temperate zone, or the extremely hot summer in the subtropics.

The parasites have often been observed to be very effective in the tropics, nevertheless, as far as it is known, they are usually biparental in reproduction.

According to our observations in Cuba in 1965, which naturally need further support if they are to be applied to other tropical districts, no aestival or hibernal diapause has been observed both in the aphids and parasites. Although there is a deep influence on both the groups, which is, nevertheless, different in different floristic zones, of the dry and wet seasons of the year, it seem to be responsible for the changes in population densities.

4. Greenhouses may be characterized as artificially developed environments, which can be very different—as to the composition of flora grown—from the neighbouring floristic associations (for example, tropical plants grown in the temperate zone greenhouses), or it may be about the same, being somewhat different as to the growing period exclusively (field crops in economic greenhouses of the temperate zone). The main differences occur during the winter period in the temperate zone, when the country is covered with snow, no green plants appearing, short day period, etc., while there is a rather suitable temperature—usually over 20°C —in a heated greenhouse, enabling the successful growth of various mostly tropical and subtropical plants.

The composition of aphid and parasite fauna occurring in greenhouses is of a different origin. Generally, it includes typical greenhouse species, which are mostly of tropical origin, or it may represent members of environmental communities that invaded the greenhouse usually during the spring-summer-autumn period and found this environment suitable for existence.

The short day of the winter period in combination with a convenient temperature represents very useful conditions for various aphids of tropical origin exclusively, which are most numerous and cause damage just during the winter.

There is no doubt that the artificial conditions, which are so different from those in the open, may also influence the parasites as to the occurrence of arrested developmental periods. According to our observations, aphid parasites (various species) have been found to occur in greenhouses during the winter as well, being rather effective in some cases. Nevertheless, no more detailed studies on this and allied problems have been undertaken to date.

— Vertical distribution — Vertical zonation of floristic associations has—as is generally known—similar laws as the North-south horizontal zonation in distribution. For instance, boreal communities such as tundra, forest tundra, etc., which occur in certain latitudes in Europe, may also be found in the higher altitudes in the mountains in Europe and the Caucasus, etc. Similar climatic conditions generally therefore occur in a floristic zone irrespective of whether it occurs in the lowlands in the north or in the mountains in the south.

As both diapause and quiescence are conditioned at first climatically, either via host biology peculiarities, or through direct response of the parasites to climatic influences, both horizontal and vertical zonation seem to exhibit the same characteristics as to the state above mentioned.

Although comparatively little has been known about these phenomena, we may at least summarize our knowledge, some examples being mentioned in this connection:

It seems that in the case of parasites of dioecious aphid species, the obligatory

aestival-hibernal diapause, similarly as hibernal quiescence, does not seem to be vertically dependent (in the temperate zone). For instance, aestival-hibernal diapause cocoons of *Ephedrus persicae* have been found both in the lowlands, submountains and mountains in C. Europe (Czechoslovakia) as well as in the proximity of upper tree limits in Italy (Alps) or in the close neighbourhood (Yugoslavia, Alps) at an altitude of about 2500 m. Similarly, aestival-hibernal diapause cocoons of *Monoctonus pistaciaecola* have been found in the mountains of C. Asia, in the lowlands of southern Italy, and in the lowlands and submountains of C. Europe (Czechoslovakia).

On the other hand, differences as to the diapause have been found in the case of *Therioaphis trifolii* parasites (introduced) in various areas of subtropical California, due apparently to the differences in host biology, various climatic conditions, etc. (v. D. BOSCH et al., 1964).

— Influence of Quaternary glaciation (Europe) — The influence of the Quaternary glaciation has generally influenced the floristic zones in forcing them to move to the south, in eradicating some of them, re-emigration occurring in a number of cases to the north after the glaciation influence had gone. The same seems to be true of the aphids and parasites. Nevertheless, some plant species were eradicated by the influence of the glaciation, and they were unable to spread northwards into the former parts of the distribution area. Correspondingly, the aphids—the specialized species—were unable to spread either, or they have spread as anholocyclic species (*Forda* spp. in C. Europe, etc.).

The comparison of biological features and geographic distribution of separate parasite species has shown that diapause and quiescence represent responses to the given type of climate; the Quaternary glaciation does not seem to have any basic effect on them as they apparently had occurred before this period. A clear example may be mentioned here: *Monoctonus pistaciaecola* is a typical member of the Mediterranean faunistic complex, which is distributed over the Mediterranean, Crimea, penetrating to C. Asia and C. Europe. It seems to be a very ancient complex. In the southern areas, the parasite species mentioned attacks the leaf-curling aphids of the genus *Pemphigus* and *Forda*. Aestival-hibernal diapause cocoons were found in samples from the district mentioned above. Nevertheless, in the northern parts of the area—due to the absence of *Forda* species as leaf-curling aphids (they are anholocyclic, living on roots in C. Europe)—it attacks only the *Pemphigus* species, the diapause cocoons being very commonly found there, too. This may be classified as a primary adaptation of the parasite to the host life-cycle (leaf-curling aphids of certain groups), which has outlasted the faunal migrations and changes caused by the Quaternary glaciation in C. Europe. The mentioned example of obligatory aestival-hibernal diapause shows the apparent and very ancient host-parasite relationship as to parasite adaptations to the seasonal occurrence and life cycle of the host.

— Parasite fauna. As is recognizable from the changes in the life-cycle of aphids with respect to their distribution, there is no doubt that also the parasite adaptations, both diapause and quiescence, will possess similar features. This means, and it has been mentioned earlier by various authors (v. D. BOSCH et al., 1964) that arrested developmental stages are area dependent phenomena. They must be considered as typical features of the biology of parasites in a certain area, being of course specifically dependent. They may change in various parts of the total distribution area or they may not. An example may be mentioned showing simultaneously the importance of an arrested development state's occurrence in the parasite in a certain area in case of parasite introduction exclusively: according to HAGEN & SCHLINGER (1960) *Aphidius smithi* does not apparently have a diapause, being active throughout the year if aphids are present. This seems to show that the parasite populations introduced have

been collected in a district where such conditions have occurred. However, the lack of diapause does not allow the parasite to survive the hot summer period connected with the aphid's absence that occur in some interior parts of California. On the other hand, the lack of diapause has not prevented the successful introduction of the parasite to Hawaii, where the tropical climate enables the continual occurrence of the aphids.

Photoperiodicity is without any doubt an important factor influencing the occurrence of arrested states in the parasites. According to DE WILDE (1962), there is an increasing amount of data showing that the photoperiod is one of the most important isolating factors in intraspecific geographical differentiation and, consequently, in insect evolution. Photoperiodic response in local strains of an insect species may differ according to the geographical latitude at which they occur without being accompanied by characteristic morphological features. Such strains may differ: (1) in intensity of photoperiodic response, (2) in effect of temperature on response, (3) in critical photoperiod. With increasing latitude, local populations of insects generally tend to be more and more univoltine, the strains of high latitude often showing obligatory diapause. Moreover, a photoperiod-induced diapause tends to be more intense in populations inhabiting high latitudes. Research of this trend is a matter of the future in the case of aphid parasites.

— *Seasonal history, host specificity.* Factors influencing the distribution and host specificity seem to be the main key factors in understanding the diapause and quiescence in parasites.

Research studies on the host specificity of parasites with respect to the evolution of both the groups have shown that it is determined by two main factors: (1) By the habitat, (2) by the presence of suitable host(s) in this habitat. As to the host suitability, the taxonomic relationship as well as the biology, mode of life, etc., of the aphid, play an important role of various mutual significance and influence (details, see: Host specificity).

With respect to the presence of diapause and quiescence it is necessary to stress the importance of the habitat in connection with aphid biology to understand the seasonal role of both the phenomena mentioned. As we have shown in the geographic distribution paragraph, the parasites are attached to certain floristic zones, and this feature also basically determines their geographic distribution. The parasites do not alternate the kinds of habitats during their occurrence in the season.

The aphids, on the contrary, often alternate the kinds of habitats during the season. The obligatory migration, connected with the habitat alternation, is lacking in some groups of aphids (Lachnidae, Chaitophoridae, Callaphididae); in other groups there is an obligatory migration, nevertheless, there is no habitat alternation (Adelgidae); in other groups, there is obligatory migration connected with the habitat alternation as a necessary part of their life cycle. The facultative migration, representing the alternation of host individuals (or some parts of them) of the same host species in the same type of habitat is commonly widespread among the aphids. Various kinds of habitats exhibit a various degree of stability as to the temperature and R.H. conditions in accordance with seasonal changes. Better to say, the biology of aphid species is deeply influenced by the climate in various parts of their distribution area, for example, it is a common feature that some species are dioecious in northern parts and anholocyclic in southern parts of their distribution area, etc. Therefore, diapause in parasites has developed as an indirect seasonal and area-dependent response to: (a) host presence in the habitat for a certain part of the season, host absence due to its migration then follows. Examples: *Ephedrus persicae*, which is dependent on the occurrence of leaf-curling aphids during spring in the temperate zone (C. Europe).

(b) Host presence in the habitat in a suitable stage at a certain part of the season, the

suitable stage then protected against attack (galls), host absence due to migration then follows. Example: *Monoctonia pistaciaetola*, restricted to the period when fundatrices of its hosts occur, their progeny being protected against parasite attack by their occurrence inside the galls, the emigration of aphids following after the opening of the gall.

(c) Host presence in unsuitable stages for parasite attack during a certain part of the season. Example: Parasites of *Drepanosiphum platanoides*, *Periphyllus*-species, in deciduous forests habitat (C. Europe).

(d) Host presence either in suitable stages (more or less numerous), climatic conditions during a part of the season not suitable for parasite active life. Example: Some introduced parasites of *Therioaphis trifolii* in some parts of California, parasites of *Sitobium*-species, etc., in the subtropics (Europe).

Quiescence in the parasites may be classified as a direct seasonal and area dependent response of a parasite to unfavourable environmental conditions occurring at certain periods of the year. Example: Hibernial quiescence in various parasites in temperate zone of Europe.

Generally, it seems that obligatory diapause is less developed in widely specialized parasites, while the species more strictly specialized—both taxonomically and ecologically—seem to exhibit a higher percentage of this state's occurrence.

Facultative seasonal diapause in parasites seems to be typical for the dry subtropic zone conditions.

In addition, it is necessary to note that the method of taking samples is of great importance for ascertaining the occurrence of diapause cocoons in aphid parasites. If the samples are taken too early, too late or at irregular intervals, there is a possibility that no diapause cocoons will be found or an untrue period of their occurrence may be ascertained. For example, (see STARÝ, 1962) diapause cocoons have been mentioned as occurring in May, June and July in *Ephedrus persicae* in Czechoslovakia. Nevertheless, they are apparently produced at the beginning of spring exclusively. They may, however, be found in the curled leaves for the rest of the season among the living aphids (Results of discussion with Prof. SEDLAG, Dresden, unpubl. notes).

—*Interspecific relations.* There is no doubt that the best type of synchronization of host and parasite seasonal occurrence is the continual occurrence of both of them throughout the year in a certain type of habitat. Such cases are known from certain areas where the climatic conditions enable the occurrence of green plants continuously, enabling the occurrence of aphids and their parasites simultaneously.

Nevertheless, some environmental conditions—both climatic and peculiarities of host life-cycle—have stimulated the appearance of certain adaptations in the parasites. Parasite species that were unable to develop such adaptation have been forced to occur in such conditions of environment where such adaptations were not necessary. For example, *Aphidius smithi* occurs in such areas in California, where there is no seasonal host absence due to the hot summer conditions, as it is unable to survive such a period in an arrested developmental state (HAGEN & SCHLINGER, 1960).

One group of adaptations—states of arrested development enables the parasite to survive a certain period of the year when the environmental conditions are unsuitable for its development either due to direct climatic influences, or due to the absence, scarcity, or unsuitable stage existence of the host.

Generally, these periods of arrested development may be classified as suitable for the parasite in its interspecific relations with other parasites and natural enemies. Aestival diapause, aestival-hibernial diapause, hibernial quiescence, whether being a closer adaptation of the parasite to the host life-cycle or not, all these states have one common feature: they enable parasite existence in a certain habitat in which the host

occurs or will occur after a certain period in a stage (mode of host life, etc.) that is—due to various reasons—suitable for the parasite's attack. Parasites that do not exhibit such a kind of adaptation cannot succeed in this case and have to adapt themselves in another way.

The seasonal occurrence and adaptations of the two introduced parasite species of *Therioaphis trifolii* in various districts of California may be mentioned in this connection; due to the various ecological optima, the species are successful in inter-specific relations to a various degree in close dependence on the given district and its climatic conditions (V.D. BOSCH et al., 1964). *Trioxys complanatus* may or may not carry on vigorous activity in wintertime. In most areas it commences intensive activity in early spring after emerging from the diapause induced the previous summer. Depending on the area, this activity may continue through spring and summer and on into the autumn. Intensity of autumnal activity obviously depends on the degree of diapause induced in the summer and, of course, on the abundance of suitable aphid hosts. If summer temperatures are sufficiently high, a substantial percentage of the population passes into diapause, and there may be essentially no resumption of activity until next spring. This would be particularly true if aphid hosts were scarce in late summer and autumn. But if there is a limited diapause and aphid hosts are available, activity can be continuous through summer, autumn, and into winter. Furthermore, where there is a carry-over of this parasite into winter, it will continue to reproduce as long as aphid hosts are available for it and minimum temperatures are not lethal. In the warmer areas wintertime activity can be continuous and intensive. *Praon exoletum* is active principally in springtime and late summer and autumn. At best, it is only very feebly active in the hibernial period since the bulk of the population passes into diapause in autumn and early winter. Its emergence from diapause occurs in early spring, and there is a flourish of activity until early summer when the wasp becomes scarce. This appears to be a product of host scarcity and the adverse effects of hot weather. In this connection, direct lethal effects of high temperatures on larvae, pupae and pre-emergent adults of this parasite have been observed in some districts of California (SCHLINGER & HALL, 1960). There is no evidence that aestival diapause occurs in this species. With the return of cooler weather in late summer and autumn, the parasite gains reproductive momentum and reaches a second peak of activity in the autumn, after which it fades away as the bulk of its population passes into hibernial diapause (V.D. BOSCH et al., 1964).

When the seasonal occurrences of both the parasite species in certain areas of California that exhibit conditions of aridity and high temperature in summertime are compared, there is no doubt that *Tr. complanatus* is more successful just owing to its ability to survive the lethal summer temperatures in an aestival diapause state; the hibernial diapause of *Praon* does not seem to be apparently advantageous, while the lack of aestival diapause is clearly disadvantageous.

There is no doubt that under other ecological conditions *Pr. exoletum* might become the predominant species just due to its hibernial diapause. For instance, in districts with mild summer and severely cold winter conditions the hibernial diapause (or quiescence) would be very advantageous (V.D. BOSCH et al. 1964)

— *Dispersal of cocoons.* Both diapause and quiescence cocoons represent primarily dead mummified aphids and for this reason they may be found at first among the living aphids, near the aphid colony, etc., being dispersed in the usual way as the other non-diapause and non-quiescence cocoons.

There are nevertheless several features that may separate the cocoons into several groups:

It is a common thing that with the growing of the top of the plant, which is

usually attacked by the aphids, the latter follow the growing parts and move gradually higher and higher; the mummified aphids are immobile so that they can soon be found remaining on older leaves. This behaviour may be observed in almost all the aphids that attack some quickly growing parts of plants, being less apparent in trees, etc. SCHLINGER (1960) when studying the biology of aphidid parasites of *Macrosiphum rosae* in California, gives a nice description of the gradual occurrence of diapause and non-diapause cocoons on the leaves of various age. Similar observations seem to be true for the parasites that attack this aphid in Europe as well (*Aphidius rosae*, *Praon volucre*), except for the lack of diapause cocoons in the mentioned species.

If the significance of diapause and quiescence for the parasite is dealt with there is no doubt that the primary function of these stages is to survive a certain unsuitable period in a suitable stage. This means, the parasites survive the period until the host appears in the same habitat again and the parasites may attack it. There are nice examples known to illustrate this adaptation—leaf-curling aphid parasites, parasites of *Drepanosiphum*- and *Periphyllus*-species, i.e., all the mentioned examples of parasite adaptation to the arrested development period of the host, all of them being mentioned earlier in a more detailed way.

There is in general no difference between diapause and quiescence from this point of view. As to the dispersal of diapause and quiescence cocoons, they at first occur among the other aphids, nevertheless, later in the season they remain on a plant while the aphids have often migrated from the habitat. Thus, we may find diapause cocoons of *Ephedrus persicae* in old leaf-curlings in the late spring when there are no more aphids present on the trees, etc.

However, certain differences as to the degree of usefulness and adaptation may be found in separate cases:

Such species, which spend the diapause state—depending on the host—in the close neighbourhood of the host colonies or specimens, may find the host to be really present after their diapause state is broken, this being usually somewhat later than the break of the host diapause. These are the cases of aestival diapause of parasites of *Drepanosiphum*, *Periphyllus*, etc., aphid.

Other species, such as *Ephedrus persicae*, have to spend a year in a similar habitat where the host is expected to appear in the following year. Their position is, therefore, somewhat less advantageous.

Quiescence cocoons are mostly found at the very same places i.e. habitats, as their hosts. This is easily to be understood because of the main features of the (hibernal) quiescence state: the aphids as well as the parasites occur on the plants until they enter the quiescence state due to the influence of the cold period. A number of examples could be mentioned: *Brevicoryne brassicae* and *Diaeretiella rapae*, *Acyrtosiphon pisum* and *Aphidius ervi*, in Europe, etc.

In some cases, the oviparous generation of the aphids occurs in some special parts of the plants where they then deposit eggs. Oviparous apterous ♀♀ of *Aphis fabae* lay their eggs on the younger branches of *Euonymus europaea* (C. Europe) in the late autumn; they are still attacked by the parasites (*Ephedrus plagiator*, *Praon abjectum*, *Trioxys angelicae*) and thus the mummified aphids (hibernal quiescence cocoons of the parasites) may be found on these branches as well in the proximity of the laid eggs. As the sexual progeny occurs for a certain period earlier on the old leaves, it would seem that the parasite larvae "prefer" the branches instead of the leaves to spin the cocoon on.

A similar case has been observed by V.D. BOSCH et al. (1962) in the case of *Trioxys pallidus*, a parasite of *Chromaphis juglandicola*. In the autumn, they also observed an apparently greater number of quiescent ("diapause") mummies on the bark than on the

twigs; this has been caused by the parasitization of the aphid oviparous ♀♀, which carried the parasites within their bodies on the woody parts of the trees due to their instinct to move off the leaves to their ovipositional site.

The dispersal of diapause and quiescence cocoons, therefore, may be generally classified as being very poor, being restricted more or less to the habitat in which the aphids have occurred before migration, seasonal diapause, or quiescence.

- *Hyperparasites.* Principally, hyperparasites are more important with the advance of the season. Early in the season the aphids begin to appear, later on the aphidiids (primary parasites), being then followed by the hyperparasites (secondary and tertiary parasites). The significance of hyperparasites is different in individual cases. Little is known about the seasonal history of hyperparasites, with respect to the arrested development periods of primary parasites exclusively.

According to SEDLAC's (1964) observation, the hyperparasites appear later in spring than the primary parasites (*Diaeretiella rapae*, Germany). They may cause, therefore, a decrease in number of hibernating parasites as well as of their progeny in spring. This observation seems probably to be true, also in the greatest part of parasites that spend winter in a hibernant quiescence state, the emergence succession of primary and secondary parasites being apparent if samples at regular intervals are taken from colonies of various aphids and reared in the laboratory during the spring (*Aphis fabae*, etc.).

The seasonal history of hyperparasite species that attack aestival-diapause and aestival-hibernal diapause cocoons of parasites seems to be more complicated. According to our observations, hyperparasites emerged from aestival-hibernal diapause cocoons of *Ephedrus persicae* in the spring of the following year; this means that they enter diapause under similar influences as the primary parasites do.

Similarly, hyperparasites of primary parasites of *Periphyllus* and *Drepanosiphum* aphids were observed to occur in spring and in autumn exclusively, this again in connection with the seasonal history of the primary parasites.

Although further detailed observations are necessary, it seems that the hyperparasites are well synchronized with the appearance of the primary parasites, which they may attack.

Considerations of quite an opposite significance have been made by SCHLINGER (1960), when studying the factors influencing the effectiveness of primary parasites—the aphidiids of *Macrosiphum rosae* in California: two groups of secondary parasites have been found to attack this aphid. Parasites of the first group (*Pachyneurou siphonophorae* ASHMEAD and *Asaphes californicus* GIR.) attacked the primary parasites (*Aphidius* and *Praon* spp.) and emerged readily from the non-diapause and diapause cocoons of both the hosts. The second group of secondary parasites included several species of the cynipid *Choripis*, and the encyrtid *Aphidencyrtus aphidivorus* MAYR: emergence during the season was from non-diapause cocoons only. According to SCHLINGER the availability of a large number of diapause cocoons as well as a smaller number of non-diapause cocoons throughout the entire season in which the secondary parasites may oviposit is the cause of abundant hyperparasitism of the aphidine populations, the secondary parasites being quite detrimental to the effectiveness of the primary parasites. This secondary parasites effectiveness seems also to be a result of their wide host range (SCHLINGER & HALL, 1960).

As the primary-secondary parasites relationship is of great significance for biological control, corresponding research is highly recommended.

- *Induction and termination.* Comparatively little is known about the diapause and quiescence as to its induction from laboratory experiments (see: MESSENGER & FORCE, 1963, FORCE & MESSENGER, 1964). Besides such valuable records, we have used our

field observations on the biology of parasites, certain outlines of further laboratory research, which has both to check and complete the field observations.

In accordance with peculiarities in their biology, the aphidiid parasites seem to exhibit somewhat peculiar features, which differentiate them from the other cases of diapause known in the parasitic Hymenoptera. The diapause in aphids is mostly connected with the appearance of a peculiar progeny, in which the arrested state period is spent. Nevertheless, the parasite enters diapause as an internal parasite of an earlier host progeny so that there cannot be any influence of the diapause of the host on the diapause of the parasite during the duration and termination of the diapause. For this reason, this kind of diapause cannot be placed as a parallel of cases of diapause in the parasites of Lepidoptera, etc. Similarly, the basic thesis of SALT (1941) that "growth of the parasite is delayed if the host insect enters diapause but is uninterrupted if the host develops without arrest" cannot be applied in our case either. This supports a generally known thesis that diapause in parasitic entomophilous insects assumes many forms.

In our opinion it seems that the degree of influence of various factors in arrested state development is not equal in all the parasite species, certain peculiar features having apparently developed in obligatory diapause as an adaptation to the host life-cycle.

— Diapause — Diapause may be induced in any developmental stage (DE WILDE, 1962). Naturally, it seems to be induced in such a stage which would allow the given or the other stage—that enters diapause—to be the most suitable for survival of a given period of unsuitable environmental conditions. As both diapause and non-diapause cocoons may often be found in the same or different aphid colonies at the same time, it would seem that diapause is induced either in the parasite ♀ or in lower instar parasite larvae, while the last instar larva or prepupa enters diapause (= responsive stage). The sensitive stage, nevertheless, seems to be the low instar larva as some experiments (FORCE & MESSENGER, 1964) have shown that last instar larvae of parasite entered diapause after egg—last instar larva instars being exposed to certain temperatures (and photoperiod) influences. Although the photoperiod has apparently also a rather deep influence on the induction of the diapause, little has been known about these phenomena in the aphid parasites. The stage sensitive to the photoperiod has not been determined in aphid parasites up to now. Generally, sensitivity to the photoperiod is never extended to the whole life-cycle. All stages except the pupa may be receptive, but in most cases sensitivity is intensified in a limited number of stages or instars. Moreover, sensitive and responsive stages are mostly different (DE WILDE).

As to the action of the photoperiod, in some cases it may be rather complicated in aphid parasites, which represent parasitic forms. The direct influence of the photoperiod on aphids is generally known. Nevertheless, in some cases the influence of food plant response to change of photoperiod on aphids seems to be inevitable (see: subterraneous and superterraneous forms of the same species, after HILLE RIS LAMBERS, see: DE WILDE, 1962). In other cases, changes in the physiological state of the host may confuse the photoperiodic effect (DE WILDE).

In parasitic insects, development is, in many cases, dependent on the physiological state of the host. In some instances, however, parasites have their own independent photoperiodic responses (DE WILDE).

1. Direct influence of temperature and photoperiod. Laboratory observations undertaken by FORCE & MESSENGER (1964) have shown that diapause in *Praon exoletum* and *Trioxys complanatus* is induced by certain temperature conditions (and apparently by the photoperiod as well). The host aphid was found to remain active while the

parasites fell into diapause. The influence of environmental factors via host aphid state is certainly untrue in such cases, the parasite responding directly to the environmental influences. The diapause is apparently induced in lower instar larvae that live inside the living host aphids, as the diapause has been induced experimentally by the exposure of parasitized aphids to experimental conditions, the parasite females being however reared in suitable environment.

Similar experiments have been undertaken by WIACKOWSKI (1960, etc.) using *Aphidius smithi*. *Trioxys pallidus* (v. D. BOSCH, 1962), spending a part of the summer period in an aestival diapause state in California, seems to represent a similar case of direct response of a parasite to unsuitable environmental conditions via diapause state.

Apparently a number of other cases might be mentioned, including mostly aestival diapause cases ascertained as occurring in various parts of the subtropic belt.

2. Seasonal lack of hosts as a facultative diapause inducing factor. The seasonal dependence of the parasite on the density of host population present in a certain season of the year has been mentioned by some American authors (see: v. D. BOSCH, 1964) as a possible cause of the parasite's entering diapause, *Trioxys complanatus* being mentioned as an example. With respect to the laboratory experiments undertaken by FORCE & MESSENGER (1964) with the same and another parasite species, it is apparent that the facultative diapause in these parasites does not depend on the population density of the host, being obviously dependent on abiotic environmental conditions. The possible coincidence of lower population density of the host aphid during the parasite diapause state seems to be caused by a response of the host to environmental conditions (abiotic and biotic), the response of the host and parasite being apparently different, the latter being shown by FORCE & MESSENGER in the laboratory tests.

Similarly, v. D. BOSCH (1962) has mentioned aestival diapause in *Tr. pallidus* as a phenomenon enabling the parasite to survive the summer period, when the host may be extremely scarce or when climatic conditions may become highly unfavourable. Unfortunately, we have no records on the occurrence of aestival diapause of this species in Europe. Nevertheless, if the diapause existed, it apparently would not be caused by the scarcity of hosts, as the parasite attacks a number of dendrophilous Callaphidid species.

3. Seasonal lack of hosts as an obligatory diapause inducing factor. In this case, the aphids emigrate from a given type of habitat due to the obligatory host plant alternation. The parasite is adapted to a certain mode of life which the aphids exhibit on primary host plants, being unable to survive the period of the lack of hosts for the rest of the season; obligatory diapause is a response to such conditions of the environment. *Ephedrus persicae* may be mentioned as an example. In this case, there is no fixation to a certain strictly time-restricted progeny. All the forms occurring in curled leaves may be attacked; the fundatrices are naturally parasitized comparatively rarely and the fundatrigeniae more frequently, due to the various temperatures conditioning the aphid and parasite development (overwintering parasite progeny appearance).

Although diapause is an obligatory adaptation to the host life cycle, it seems to be somewhat strange that the percentage of diapause cocoons occurrence is not equal, varying almost from the total number to a low percentage when compared with the non-diapause cocoons. This shows that a certain part of the population remains in a non-diapause state: it is a question, however, what is the further fate of these parasites as we have not found *E. persicae* attack any aphids later in the season (in summer) in C. Europe.

Similarly, it is peculiar that the diapause cocoons may be found approximately at the same time irrespective of host species attacked, a number of living aphids being present in such colonies as well.



Fig. 241. *Periphyllus* sp. on *Acer platanoides*. Aphids producing diapause nymphs. Inset: detailed.

Fig. 242. Diapause adult aphids (*Drepanosiphum platanoides*) on underside of leaf – *Acer pseudoplatanus*. Left and above – whitish yellow diapause cocoons of parasites

According to HODEK's (1966) classification of diapause in aphidophagous insects, the above mentioned case would fall into the group of "daring" species, which sacrifice a part of the population in order to make use also of a period uncertain as to the development of the species.

4. Seasonal lack of suitable host progeny as an obligatory diapause inducing factor. This case seems to be a rather isolated one, the parasite being apparently dependent on the occurrence of a certain progeny of the host. The induction of diapause in the parasite via its host aphid seems to be rather probable in this case.

Monoctonia pistaciaecola may be mentioned as an example. It attacks only the fundatrices of its hosts, diapause cocoons exclusively developing in the parasite progeny. It means that the parasite is apparently influenced by the environmental abiotic conditions for a very short time—it really seems that this influence is probably rather short, the conditions seemingly not being very different from the abiotic conditions which occur in the later period of the season. Nevertheless, in the later periods the parasite female would fail to parasitize the fundatrigeniae progeny of the fundatrix as the aphids are closed inside a gall.

Another case seems to be that of the parasites of *Periphyllus* and *Drepanosiphum* species in C. Europe.

The *Periphyllus* aphids spend the summer period in diapause lower instar nymphs, which are unsuitable for parasitization. The diapause in parasites is apparently induced when they parasitize an earlier host progeny, as the diapause parasite larvae occur simultaneously inside mummified aphids that belong to the earlier progeny, while the diapause nymphs of the aphid start to be produced by unparasitized aphids. (Fig. 241).

The *Drepanosiphum* aphids exhibit the peculiar behaviour of adults (see above)—a spacing which is in reality a summer diapause. The parasites spend this period inside mummified aphids of earlier progeny, the diapause being therefore induced during the parasitization of the earlier progeny of the host (Fig. 242).

According to HODEK's classification (1966) of diapause in aphidophagous insects, the above mentioned cases seem to fall into the group of "cautious" species, which prefer a safe developmental cycle even though the number of generations is usually

limited to one; presumably food has been more influential than abiotic factors in this process.

5. Induction of diapause through less suitable host parasitization. SCHLINGER (1960) and SCHLINGER & HALL (1960) reported a case of diapause through less suitable host parasitization in *Macrosiphum rosae* parasites in California. Several parasites observed entered diapause when parasitizing *M. rosae* while they were mostly found to develop normally—without arrested states—when parasitizing other aphids. The authors classified this case as an apparent result of poor parasite-host synchronization.

The opinion mentioned above does not fit in at all with the classification of diapause in aphid parasites as a response to the influence of abiotic factors as well as a response—adaptation—to the host life cycle. Seasonal diapause in the parasites of *M. rosae* in California could be generally understood as a response to certain unsuitable abiotic conditions, this being a common feature of dry subtropics parasite fauna, nevertheless, no such host selection would apparently occur. The parasites mentioned, too, are not specialized parasites attacking *M. rosae* as their single host in California. This is also recognizable from the origin of the *M. rosae*, which represents an introduced species in California.

6. Conclusive notes. Diapause is apparently caused by the influence of the abiotic (temperature and photoperiod) as well as biotic (host life history) factors.

Obligatory diapause seems to be primarily an adaptation to the host life cycle although apparently induced previously by temperature and photoperiod conditions. Facultative diapause seems to be a specific response of the parasite to unsuitable environmental (abiotic) conditions, the host life cycle having apparently very little to no significance.

Thus, diapause may be classified as a result of parasite adaptation for synchronization with the host development as well as for the survival of a period when unsuitable environmental abiotic conditions occur.

We have very limited records on the termination of diapause. Generally, observations have shown that parasites emerge from diapause cocoons at the time when they may find the hosts in the given type of habitat (field observations only).

In the case of *Trioxys complanatus* in California (SCHLINGER & HALL, 1961), the individual of any one diapause population apparently emerge approximately at the same time even though these individuals entered diapause over a long period of time, often of several weeks. The response of all the individuals to the stimuli that cause the termination of diapause takes place regardless of when they entered the diapause.

Field observations are not of much value as to the establishment of the termination of the diapause; field records may show only the period of emergence of the parasite adults from diapause cocoons. There undoubtedly exists a period between the termination of the diapause state, which is spent in last instar larva - prepupa stage, while pupation and pupal development must follow before the emergence of an adult from the diapause cocoon, this period being under the possible influence of the given temperature conditions (low temperatures prolongate such a period).

For field observations, therefore, it is perhaps better to use the indication "emergence of adult parasites from diapause cocoons" instead of "emergence from diapause".

Experimentally, after certain exposures to moisture and low temperature, the diapause had been broken and the larva pupated under warmer temperature conditions (*Praon exoletum* in California, SCHLINGER & HALL, 1959).

Generally, due to the occurrence of the diapausing stage of the parasite in a separate cocoon, there being no direct connection with a living host, we presume that

1953				1954			
Date	Total mummies	Non-emergence		Date	Total mummies	Non-emergence	
		No.	%			No.	%
July 7-14	5	0	0.0	July 27-Aug. 3	98	30	30.6
July 21-28	11	4	36.4	Aug. 10-17	44	29	65.9
Aug. 4-11	236	79	33.5	Aug. 25-30	45	19	42.2
Aug. 18-25	2231	833	37.3	Sept. 7-13	92	41	44.6
Sept. 1-8	4242	1595	37.6	Sept. 21-27	282	180	63.8
Sept. 23	3213	1623	50.5	Oct. 11	114	97	85.1
Oct. 7	1449	1344	92.8	Oct. 20	107	100	93.5
Oct. 21	1577	1551	98.4	Nov. 9	254	250	98.4
	12964	7029			1036	746	

Table 5. Overwintering of parasites of *Brevicoryne brassicae* (GEORGE, 1957).

the termination or break of the diapause is apparently caused through the influence of abiotic factors of the environment (temperature, photoperiod).

– Quiescence – Numerous field observations have been undertaken. The most instructive one seems that of GEORGE (1957), carried out on *Diaeretiella rapae* in Great Britain. At the end of the season in both the experimental years there was a considerable number of mummies from which the parasites had not emerged. The proportion of parasites overwintering in this way increased as the aphid season progressed. The gradual influence of the low temperature conditions (connected with the decreasing photoperiod not mentioned) is easily seen from the table (Table 5), where the overwintering of parasites of *Brevicoryne brassicae* is presented, the results obtained in 1953 being most remarkable. The dependence of hibernation quiescence state on the decline in temperature and photoperiod in autumn has been also observed by HAFEZ (1960) in the same parasite species.

The quiescent state ceases to exist after the unsuitable environmental conditions stop occurring, the normal development of the parasite then continuing. Both laboratory and field observations support this general rule. According to HAFEZ (1960) the hibernation (i.e. hibernation quiescence) in *Diaeretiella rapae* could be easily broken by exposing the mummies to room temperatures and a long photoperiod. Similar conclusions were made by TREMBLAY (1964) in *Lysiphlebus fabarum*. Our own laboratory studies on *Aphidius megourae* hibernation may be presented in addition (STARÝ, 1964, 1966) as well.

– Significance – As mentioned above, the arrested state periods (diapause, quiescence) in aphids are classified as an indirect or direct response to unsuitable environmental conditions, being equal as to their significance to aphid migration.

Generally, diapause and quiescence in parasites may be classified as either indirect or direct adaptation for survival of certain unsuitable periods for parasite existence. Originally, the occurrence of these arrested states seems to be a phenomenon of good synchronization of the parasite-host occurrence and vice versa (see: Parasite introductions). The ability of a parasite species to survive unsuitable conditions of the environment, which are survived by its host as well, enables the parasite to occur in better synchronization with the host's occurrence. On the contrary, if a host species is able to survive certain conditions and the parasite is unable to do so, such a relationship means the lack of a parasite species in a given district of the distribution area of the host.

☞ Obligatory diapause in the parasites seems to be a phenomenon of rather close

dependence of a parasite on host development, a matter of close specialization, which restricts the parasite's action to a part of the season when the suitable host stages occur.

Facultative diapause seems to be an intermediary phenomenon as to its significance for parasites.

There is a commonly occurring opinion (KENNEDY, 1966, etc.) that the diapause state has a protective significance against natural enemies' action. We have to deal with parasites exclusively, nevertheless, we shall try to show on various examples that such an opinion seems unjustified.

As mentioned above, the parasites have apparently adapted themselves to the occurrence of the arrested state in their host's development, either by a wider host range, or by the occurrence of corresponding arrested states. From the parasite-host relationship point of view it is apparent that a wider host range enables the parasites to occur in a given habitat throughout the whole time until the hosts appear again in this habitat, the parasites then infesting them. Similarly, the occurrence of arrested states in the parasites enables them to appear again—this being apparently a phenomenon of synchronization in host-parasite occurrence—when the break of hosts' diapause occurs and the host later appears in a stage which is suitable for the parasite attack.

In cases of poor occurrence of host-parasite synchronization different response of host-parasite may be found to environmental conditions (see *Praon exoletum* and other parasites of *Therioaphis trifolii* introduced to California).

As an addition to this paragraph, we shall deal here with *Drepanosiphum platanoides* aestival diapause. Aestival diapause in this aphid has been mentioned to have a possible defensive function against natural enemy action (KENNEDY, 1966). According to observations of British authors (see KENNEDY) *Drepanosiphum platanoides* is frequently seen in the summer in Gr. Britain in large numbers on the underside of sycamore (*Acer pseudoplatanus*) leaves in the form of winged adults only, earlier instars being absent. This feature has been classified as being caused by the entering of adults in the aestival diapause. Peculiar spacing has been observed to occur in the aphid groups, whether the individuals on a leaf are many or few. In a series of experiments on leaves and on glass it was confirmed that these aphids are gregarious, although they repel one another up to a certain distance. This is the distance at which they do not actually touch any neighbour as long as they remain motionless, but do just touch if they move their antennae which is their first response to any object moving near. Further experiments, using artificial tactile stimulation with a bristle, showed that strong stimulation of this kind causes an aphid to move away, but weak stimulation of the same kind (resembling that which the aphids give each other at their standard spacing) arrests it, and brings about aggregation. When one member of a grouping moves owing to stimulation of some kind including that from predators (parasites not mentioned—author's note), its neighbours are activated in turn and the disturbance is propagated through the group. It is suggested, therefore, that the main advantage of gregariousness and of the mutual stimulation and diapause that it entrains is the increased immunity from enemy attack which converts the entire population into agile winged adults.

The above mentioned observations—as to the aphids—correspond with our own observations carried out in Czechoslovakia. Naturally, we have dealt with parasites exclusively, while the predators action—mentioned by KENNEDY—has been omitted. Although no detailed observations have been made as to the separate parasite species, the seasonal occurrence and host specificity features of the parasites of *Dr. platanoides* show that there is apparently a close synchronization in host-parasite seasonal history. *Dr. platanoides* is a Callaphidid species, the latter group seems to be a case—apparently

due to the lack of obligatory migration of its representatives—where there is a close host-parasite relationship in phylogeny. The parasites of Callaphidid aphids are mostly strictly specialized species, both to the habitat and hosts, and for this reason a close relationship of parasites to the seasonal occurrence of their hosts may be presumed. Really, the three parasites known to occur in Europe, *Trioxys cirsii*, *Monoctonus pseudoplatani* and *Dyscritulus planiceps*, have been observed to occur in spring and in autumn only, while they are absent in nature in the summer, diapause cocoons being found only. This shows the existence of adaptations of parasites seasonal history to their hosts. The adaptive function—i.e. apparently the developmental causes of the summer diapause in parasites—seems to be found when the host specificity of parasites is classified: *Trioxys cirsii* and *Monoctonus pseudoplatani* apparently attack the low host instars, as the last instar aphids are usually found to be mummified. As such low instar nymphs of aphid host occur only in spring and in autumn, the parasites being strictly specialized, the latter have been forced to adapt themselves to the seasonal history of their host—by the developing of arrested state periods (summer diapause) in their seasonal occurrence. The third parasite species—*Dyscritulus planiceps*—apparently attacks higher instars or alate adults of the hosts as only alate specimens of this host aphid may be found to be mounted at the top of the parasite's cocoons. This parasite is therefore well adapted to the infestation of adult aphids, so that it might infest the adult aphids that occur during the summer months. Nevertheless, there must be a certain factor—specific behaviour of the aphids, their arrested state, etc.—which causes the parasite to occur only in spring and in autumn in a similar way to the other two parasite species previously mentioned.

Although more detailed observations undoubtedly are necessary, our field observations on the peculiarities of parasite biologies have shown, that the summer diapause of *Drepanosiphum platanoides* does not seem to mean a protective function against the parasite action, as both the groups spend a certain part of the season in an arrested state.

Our opinion, besides the field observations, has been supported by the almost identical case—as to its significance—of that of *Periphyllus* spp. and their parasites. In this case, a similar seasonal adaptation has apparently developed in the parasites as an adaptation to the summer period when the host aphids occur in diapause nymph stages, which are unsuitable for parasitization.

—*Natural limitation.* Theoretically, the best state for the successful natural limitation of an aphid by a parasite seems to be such a state, when the aphids and parasites occur in a certain type of habitat throughout the year, well established synchronization being developed. We know such cases really to occur (stable environments namely) and moreover they seem to be common.

Nevertheless, the obligatory migration of aphids as well as different responses of host and parasite to unsuitable environmental conditions have caused apparently deep changes, so that various adaptations of parasites both to the host life cycle and environmental conditions may be observed to occur today.

It would appear that diapause causes the decrease of parasitization percentage and effectiveness, nevertheless, various viewpoints can be applied so that a unique conclusion may not be formed.

Obligatory aestival-hibernal diapause, on the one hand, decreases the percentage of parasitism in spring as the diapause is induced at the period of a sufficient host population density, nevertheless, on the other hand, obligatory diapause represents a greater possibility of parasite survival and its occurrence in a suitable period of the year. Otherwise the parasite would not be able to survive the period of the host absence till the next year. Naturally, such an adaptation seems to be less advantageous

than the wider host range that enables some parasite species to survive the given host absence due to their ability to attack other hosts.

Obligatory aestival diapause may be classified in a similar way.

Facultative aestival diapause seems to be useful for parasite survival of a certain period when unsuitable environmental conditions occur. If the host response is the same or at least similar, aestival diapause of parasites seems to be useful for natural limitation of aphids by parasites as it is well synchronized with the host development. On the other hand, if the parasite enters diapause and the host prolongs its active life, such a parasite adaptation may be detrimental to its effectiveness at least for a certain part of the season.

However, also in the less suitable case mentioned, facultative aestival diapause enables the parasite to occur at least at the same place as the host, which may be kept within limitation by the parasite in another part of the season, while the total lack of diapause in case of inability to survive certain environmental conditions means the complete absence of a parasite in a certain area.

— *Biological control.* 1. Pest aphid classification. Before any biological control activities are undertaken, a careful classification of the pest aphid bionomics and life-history, both in its distribution area as well as in the given country, are needed. It is necessary to know under what temperature conditions the pest will be controlled. With respect to this primary task, the biological control laboratory work with the corresponding results for field experiments is then organized.

2. Indigenous parasites and the introduced pest aphid. The fauna of indigenous parasites occurring in the given area represents a group in which members of various faunistic complexes play various roles of importance. Generally, it is a group that has developed during a long period of time, under various influences of various factors, such as geological periods, climate, flora, presence or absence of certain aphids, etc. Nevertheless, there is no doubt that just the indigenous fauna may be characterized as a group that has adapted in probably the most advantageous way to the existing conditions of environment, various adaptations being developed—both to climate influence, aphid life-cycle, etc.—in consequence.

The new pest aphid, as a new member of a certain community, falls under the influence of the biotic factor as well, i.e. also under the influence of the native parasites. Being a new aphid pest, a species that is similar taxonomically-ecologically etc., to the host of indigenous parasites, (see: Food specificity factors) we have to expect that the parasites will attack this aphid to a various degree. In some cases, they may be found rather effective, in other cases their effectivity may be insignificant. Nevertheless, we may presume that their main adaptations to the conditions of the given country will remain unchanged, and then a peculiar synchronization can develop in case of the new pest aphid- indigenous parasites relationship.

Little is known about these phenomena in more detail as, unfortunately, both the biological control objects of today—*Therioaphis trifolii* and *Chromaphis juglandicola*—seem to be taxonomically and ecologically different from the native fauna of Nearctic America, so that almost no indigenous parasites are known to have adapted themselves to these new pests. There are, however, some other pest aphids, which have been introduced into the Nearctics in earlier times, such as *Acyrtosiphon pisum*, *Macrosiphum rosae*, etc.; as they are related to the indigenous fauna, some of the indigenous parasites of the N. American fauna are known today to attack these aphids as well.

3. Selection of parasite species to introduce. Selection principles of parasite species have been dealt with in more detail in another paragraph (Geogr. distribution, biological control). The parasites are selected and later colonized with respect to

their requirements on habitats and microhabitats. At least general observations on their biology in the country of their origin have to be known to be used in a biological control program. Parasite species exhibit a specific and different optimum temperature from each other (FORCE & MESSENGER 1964). Thus, for instance, of the two introduced parasites of *Therioaphis trifolii* in California, *Praon exoletum* has been found to prefer a milder climate, *Trioxys complanatus* preferred higher temperatures, both requirements later having a corresponding influence on their distribution, spread, occurrence, diapause and quiescence in the given area of introduction, all these phenomena being of basic significance for determining the significance of introduced parasites in biological control.

4. Shipment. Diapause and quiescence may have a certain significance in shipment of parasites. According to FISCHER (in DEBACH & SCHLINGER, 1964), the occurrence of the diapause would be expected when shipping insects either between hemispheres or between sharply contrasting climates (after FLANDERS, 1944).

As for the aphid parasites, no such possibility is to be expected due to several reasons; naturally, certain knowledge is necessary before the parasites are exported by ship to avoid the sending of obligatory aestival-diapause cocoons. Usually, either parasite adults or mummified aphids containing parasite mature larvae to pupae are transported. In this case, there is no danger of the entering of parasites into diapause as the diapause would be induced in lower larval instars and cannot be caused by the immediate influence of climatic change during the transport, which is moreover rather quick due to airmail service. Better to say, no diapause may be induced in adults during the transport.

When field samples are taken and then sent abroad, no more detailed field observations on the ecology of separate species being at hand, it seems that the material collected and sent from subtropic countries during an unsuitable period might contain a certain percentage of diapause cocoons. Only a small probability of this kind seems nevertheless to occur in the temperate zone as well as in the tropics.

5. Rearings. Laboratory rearings need the selection of optimum constant temperature for successful culturing of hosts and parasites. Moreover, care must be taken with the laboratory conditions as in some cases the host optimal conditions may induce diapause in the parasite. According to SCHLINGER's observations (1960) in California, the primary parasites of aphids often enter diapause while their hosts continue reproduction. This is perhaps true for the material collected in the subtropics. Our experience, which has been mostly undertaken with temperate zone material, and to a lesser degree with the material of subtropical and tropical zones, has shown that the entering of parasites into diapause is very rare in laboratory rearings—corresponding probably to the field conditions of the corresponding zone.

6. Introduced parasites and the new environment. One of the basic conditions for the successful establishment of an introduced parasite in a new country is the synchronization of host and parasite seasonal occurrence in a given country.

Synchronization of the host aphid and parasite is of a different degree of importance in various areas. In some areas the host and parasite are able to reproduce continuously throughout the year due to favourable climatic conditions, the generations overlapping and synchronization in the seasonal occurrence is not necessary.

For example, *Aphidius smithi* in some areas of California is well synchronized with *Acyrtosiphon pisum* occurrence. On the other hand, however, this species (HAGEN & SCHLINGER, 1960) has been mentioned as being unable to survive the long periods of aphid absence, which occur in some inferior areas (hot and dry summer period). In this case, the lack of synchronization of host-parasite occurrence prevents the successful establishment of this parasite in certain areas of California.

Trioxys pallidus, a parasite imported to the U.S.A. from France and used in biological control of *Chromaphis juglandicola*, might be mentioned as an example of a different character, where the coincidental occurrence has enabled the parasite establishment. Observations made after the colonization of this species in California have shown that the parasite is temporarily synchronized with the host aphid, both aestival diapause, hibernal quiescence (= hibernal diapause of v.d. BOSCH et al., 1962) being observed. Aestival diapause enables the parasite to survive the period when *Chr. juglandicola* may be extremely scarce or the climatic conditions may become unfavourable, hibernal quiescence enables the parasite to survive the winter period when the host occurs in the egg stage.

7. Diapause, quiescence, and colonization of parasites. Although the parasites are primarily connected with certain floristic zones, and belong to certain faunistic complexes, there is no doubt that the separate species are further differentiated with respect to their requirements on the microhabitat. At least field observations made in the native country of the introduced parasite have to be at hand before the parasite is initially colonized. The colonization place has to correspond to a similar habitat of the parasite in its native country.

For example, when subsequent data on the establishment of imported parasites of *Therioaphis trifolii* were obtained, it was apparent that the separate parasite species are distributed inadequately, thus showing the existence of certain differences in the climatic tolerances among the parasites (v.d. BOSCH et al., 1964). In certain areas the climatic conditions caused seasonal diapause in the parasites, in other districts the parasites occurred throughout the year; these observations have clearly shown the area-dependent character of diapause in the case of *Praon exoletum* and *Trioxys complanatus*. The secondary observations on habitat preference have supported the preliminary observations made by one of the authors in the parasites' native home—in the Old World—where the parasite species were observed to be adapted to a hot desert climate in a different degree, *Tr. complanatus* preferring the hot lowlands. The comparison of these observations has stressed the necessity for careful preliminary examination and observation of separate habitats in which the parasite species occur in their native (or other) country from where they are to be exported. The comparison of the habitats with the similar ones of the country of colonization may result in a more or less accurate prediction of the parasite's future occurrence in the new country where it is to be used in biological control.

8. Effectiveness. The synchronization of parasite diapause with the seasonal history of the pest aphid is of basic significance in biological control when introducing certain parasite species in a new area and it may be classified from various points of view.

In certain cases, the occurrence of diapause in an introduced parasite in the period when the host prolongs its reproduction is unfavourable as it deeply influences the parasite effectiveness and enables the pest aphid to possibly reach outbreak population density. For instance, diapause is a limiting factor in the case of *Praon exoletum* and *Trioxys complanatus* in some areas of California, where the aphid is able to reproduce during the time when the parasite is in diapause, before the parasites emerge from diapause, or after the time when most of the parasites have entered diapause (SCHILLINGER & HALL, 1960). In another case, *Aphidius smithi* does not enter aestival diapause in California. For this reason, it has been found to be unable to survive the hot summer period when the aphid host (*Acyrtosiphon pisum*) is absent in some areas of California, although it may be found to occur continuously in other parts of the state where the host is present throughout the year. (HAGEN & SCHILLINGER, 1960).

These cases have distinctly shown the two sides of diapause significance for para-

site effectiveness. The relative value of diapause for parasite effectiveness has also been proved experimentally. When studying the host-parasite systems in the laboratory—*Therioaphis trifolii* and *Praon exoletum*—MESSENGER & FORCE (1963) have found that in fluctuation temperature environment averaging 21°C the parasite was effective in checking the increase of the host before the onset of plant damage. In a cooler environment, averaging 12.5°C (all other physical factors unchanged) the parasite was ineffective in preventing aphid populations from increasing to plant-damage levels. The induction of diapause in an increasing proportion of parasite progeny was one of the factors that lowered the parasite effectiveness.

These cases show that diapause may be of high significance as to parasite effectiveness, in the case that its occurrence is well synchronized with the seasonal history of the pest.

9. Arid zone problems. Biological control of aphids in an arid zone has shown that this zone exhibits certain peculiar features. The parasites in arid zone districts often spend certain periods in diapause due to the extremely hot summer. The biological control praxis has shown that similar responses of parasites have to be expected in case of the introduction of the parasites from one district of an arid zone to another (Old World—California in *Therioaphis trifolii* case).

There is another problem—that of the introduction of parasites from a temperate zone to a subtropic arid zone. Although the temperate zone parasites have usually no seasonal diapause as a response to hot climate periods (summer) such adaptation nevertheless may develop as a response to the new environment and the unsuitable conditions of the summer (facultative aestival diapause). When introducing the parasites from a temperate to a subtropic zone, it is necessary to have in mind that two viewpoints at least must be considered: the parasites have to be used in irrigated lands where the aphids usually occur throughout the year, with no lack of hosts during even the hot summer period. The introduced parasite—if capable of surviving the high temperatures—may occur throughout the year as well. There is another problem, whether or not the parasite will be able to survive the period of host absence during a hot summer period in an extremely hot and xerotherm habitat. This second question is really very important for biological control introduction praxis. In every case, it must be expected that the parasite will—as partly the California praxis shows—select the most suitable places, being absent in other places where it is unable to survive due to various reasons.

Experiments solving this question are necessary: owing to irrigation of certain districts of arid zone, new conditions have been developed, and it is possible and probable that some parasite species, although temperate in origin, might be useful in biological control in an arid zone as well. The penetration of temperate zone elements in the arid zone when following the valleys of rivers, irrigated orchards, etc. may represent a certain indication of such a probability, although being incidental.

— *Integrated control.* 1. Tillage. It has been generally recognized that short-term plantings such as vegetable crops, etc., are not very suitable for integrated control although they cannot be overlooked. In these unstable environments, which represent more or less annual communities, a stable host-parasite relationship can hardly develop. Tillage—which represents just a very typical factor destroying the whole community—is also fatal for the diapause and quiescence of parasite cocoons present in the given crop field in the autumn. This feature has been observed and mentioned by various authors—SEDLAC, 1965, etc., in *Diaeretiella rapae* and *Brevicoryne brassicae* on cruciferous crops. Similarly, STARÝ (1964, etc.) in the case of classifying parasite foci in nature has also recognized the fatal significance of tillage for a number of parasite foci; WAY (1966) also studied experimentally the influences

of overlaying of parasite cocoons by soil and his experiments have shown that tillage eradicated the parasite cocoons in the given area.

In the permanent or semipermanent communities there is almost no tillage except for some cases (clean cultivation, see below). These communities—forests, orchards, perennial fields of forage crops—have been recognized as being suitable for integrated control activities. In these habitats the diapause and quiescence cocoons spend the period before adult emergence in a more or less untouched state, except, naturally, for the general influence of abiotic and biotic factors everywhere present. For example, introduced species of parasites of *Therioaphis trifolii* may be found in winter either on the alfalfa foliage or on the ground in California (DAVIS et al., 1957).

2. Clean cultivation is a common practice used in both economic and small farmers' orchards as well as in parks, gardens etc. By this practice the surface of the soil is superficially mown to kill the weeds, for green manuring purposes, for removing the leaves fallen in autumn, etc. There is no doubt that clean cultivation in the autumn is extremely fatal to both the diapause and quiescence cocoons of the parasites. Diapause cocoons of *Ephedrus persicae* inside leaf-curlings, quiescence cocoons of *E. plagiator* on various leaves, quiescent cocoons of parasites of *Drepanosiphum*-aphids, etc., they are all taken with the leaves and destroyed by clean cultivation.

There are some exceptions, however, which are not touched by clean cultivation. *Chromaphis juglandicola*-oviparous ♀♀ in the autumn move (ovipositional instincts) onto the woody parts of the trees to their oviposition sites; they are parasitized and transport the parasite larvae in themselves, so that a number of the mummified aphids may be then found on the bark of the trees (v.d. BOSCH et al., 1962). This kind of behaviour seems to be very valuable for the aphid control, as clean cultivation cannot affect the overwintering parasite stages. Further observation in this direction is needed in individual cases, as according to our observations, this phenomenon seems to be more widely distributed among the parasites, in such species namely that occur late in the autumn and attack the oviparous aphid progeny.

Clean cultivation, therefore, is most dangerous to the parasites that pupate exclusively on the leaves.

As tillage and clean cultivation cause the lack of parasites in a given place at the beginning of the next year, thus giving the aphids better conditions to reach a higher population density and cause damage, the foci of parasites in the given orchard or field neighbourhood have, therefore, a great significance for the re-establishing of parasite occurrence in the areas mowed or cultivated. Both diapause and quiescence cocoons of the parasites represent stages that have to be protected, in a certain way to augment the parasite numbers in a certain habitat in a certain part of the season. As the mentioned stages are somewhat peculiar, integrated control activities have to be modified in a corresponding way.

3. Cutting. In some cases, cutting of plants (roses) may mean the removing of the parasite diapause cocoons from the garden. Such observations have been made by SCHLINGER (1960) when studying the parasites of *Macrosiphum rosae* in California. The cutting and removing of plants has been classified as one of the factors that lower parasite effectiveness. Mowing seems to have an identical significance.

4. Insecticides. Both the diapause and quiescence state in the parasites are spent in last instar larva to pupa inside the cocoons. In some cases, the walls of the cocoons are spun in a much thicker manner.

Observations of a number of authors have shown that the aphidid parasites are least affected by chemical treatment when being in the last larval-pupal stage inside their cocoons. The greatest part of observations has been made on non-diapause

cocoons and non-quiescence cocoons. Nevertheless, because of the similarity of the construction of the cocoons, we may assume that both diapause and quiescence cocoons will be at least as resistant to the topical and residual effects of chemicals as the normal cocoons. Better said, the parasites emerge from such cocoons after spending some time, a very considerable time, inside, and this practically eliminates the effect of the residuals, which has been found to be dangerous to the adults that emerge very soon after pupation in the normal cocoons.

— *Relative value.* The arrested states in development—diapause and quiescence—may be generally classified as either indirect or direct adaptations-responses to unsuitable conditions of the environment, through which the parasite is able to survive such a period. Both diapause and quiescence states, therefore, enable the parasite occurrence in a certain area, being of basic importance for this reason. Various summarizing viewpoints are stressed on the value of diapause and quiescence with respect to the natural limitation and control of aphids.

Diapause of every kind seems to be a valuable seasonal adaptation of a parasite to environmental conditions. Generally, its significance may be different. The disability of a parasite to survive a certain period of unsuitable conditions in a diapause state practically means the absence or failure of the establishment of such a species in a given area. On the contrary, the ability of survival in a diapause state enables a parasite to occur in a given area. From this point of view, the presence of diapause is better than the lack of it, nevertheless, an adapted parasite which could survive the unsuitable conditions without arrested period (diapause) in its occurrence seems preferable. Obligatory seasonal diapause may cause decrease of parasite effectiveness in a certain period of host occurrence, but it simultaneously means the presence of the parasite in a given habitat when the unsuitable environmental conditions cease to exist, i.e. when the host will be present again in the habitat. Facultative diapause may be rather useful if it is well synchronized with the seasonal lack of host or its presence in a rather low number in the habitat, but it may be detrimental to limitation in a certain period of the season if it is not synchronized, i.e. the host continues its active life, while the parasite enters diapause. Generally, continuous occurrence of a parasite seems to be preferable than its seasonal lack, nevertheless, a diapause state is preferable to the disability of a parasite to survive unsuitable environmental conditions. Diapause may cause—usually in case of its poor synchronization with the host occurrence—temporary gaps in parasite occurrence and corresponding gaps in limitation of the host. Such gaps have to be covered by the utilization of other parasites or other natural enemies through biological control activities.

Hibernal quiescence seems to have a positive role in establishing the occurrence of a parasite in the same hibernation quarters as that of its host. There is no doubt that if the coexistence of host and parasite system in the autumn is temporarily interrupted through the winter conditions—both members of the system being in a quiescent state during this period—the coexistence is prolonged to the next spring. This may have a great significance for the natural limitation and control of aphids by parasites. As far as we can consider from our field observations as well as from the literature records, the hibernation quarters of parasites are habitat dependent, in the same way as their seasonal occurrence. The same can be said of the aphids. The latter, however, may alternate the type of habitat during the season, while the parasites never do so. Generally, the hosts have been attacked by a parasite in the autumn in a certain type of habitat, the same hosts—or simultaneously other hosts as well, in accordance with the parasite host specificity range—are attacked in spring, be the host anholocyclic or holocyclic monoecious or dioecious species. No cases seem to be known where the parasite would be in a hibernal quiescence state, its host pro-

longing active life. The dependence of the parasite on the seasonal occurrence of its host causes the occurrence of a certain interval between the host and parasite appearance in spring, this usually resulting in a prevalence of aphids for a certain period in spring. On the contrary, so far it seems, no such prevalence may be found in the autumn, the parasites affecting the oviparous aphids as well (*Aphis fabae*, *Acyrtosiphon pisum*—Europe; *Trioxys pallidus*—California, after v.d. BOSCH, 1962). Hibernial quiescence, therefore, does not seem to be a detrimental factor as to parasite effectiveness, but it seems to be an important limiting factor (number of parasites hibernating, etc.).

— ZONES — Seasonal history in separate climatic zones may be generalized rather superficially as, on the one hand, we have a relatively poor knowledge of seasonal history of parasites in different zones, on the other hand, seasonal history of various species naturally manifests specific differences.

1. Temperate zone is characterized by cold to severe winters and mild to hot summers. Low temperatures, absence of green plant growth, etc., cause the aphids to survive winter mostly in the egg stage; the parasites develop quiescent states in order to survive. The emergence from quiescent mummies may occur during a short period (*Aphidius ervi*) or during a longer period (*Diaeretiella rapae*—SEDLAG 1964) in spring. The period of parasite emergence in spring depends perhaps also on the host range of a given parasite species. The parasites may appear in spring either almost simultaneously with the aphids (fundatrices progeny), or somewhat later than their hosts; in this case the aphids can reproduce considerably before the parasites appear. A hot summer period is mostly connected with the decrease of aphid and parasite numbers; an increase in population can be observed in the autumn. In the autumn, too, gradually more numerous quiescent cocoons appear (see above).

2. The Subtropics are characterized by mild winter and hot summer conditions. Further, there is a difference between dry and humid subtropics. Aphids and parasites occur practically perennially but obvious seasonal differences in population are observed. Hot summer conditions are rather unfavourable to parasites, causing a decrease of aphid numbers; quiescent states may be found among the parasites as an adaptation to survive such a period. Similarly, quiescent states occur also during winter periods in the colder subtropical districts.

3. Tropics. Two yearly seasons generally are recognized in the climate of the tropics: there is a rainy season and a dry season. The dry season is characterized by lack of rain, vegetation becomes poor and dry, while its growth rapidly increases as soon as the rainy period begins. The influence of these yearly seasons is obvious in the tropical steppe or savanna districts for instance being less apparent in the ever-green communities. Better to say, there is a great difference between the hot lowlands and cooler tropics at higher altitudes. Aphids and consequently their parasites too depend on the occurrence of green plants, so that they are common in the period when plant growth is active and intensive. However, there are apparent differences in the natural savanna and cultivated savanna or deforested areas; the latter districts are often irrigated and green plant cover causes the occurrence and mass-reproduction of aphids, though they may be rare in the neighbouring natural savanna. Generally, the parasites occur perennially in the tropics, manifesting changes in population density depending on the season of the year.

4. Greenhouses. Seasonal history of parasites in the greenhouses is influenced by the type of greenhouse and, indirectly, by a given climatic zone. In the temperate zone, due to climatic conditions, greenhouses are either heated or unheated during the cold winter period. In unheated greenhouses, the parasites overwinter, but, when compared with natural conditions, they may occur here actively up to later

in the autumn and emerge earlier in spring due to the microclimatic conditions that exist here. Naturally, the presence of green plants and aphid hosts is necessary for the further development of their populations. In heated greenhouses the parasites occur perennially, their occurrence, however, is strongly influenced by changes of microclimatic conditions in these greenhouses and their influence on aphid numbers. In the subtropics and tropics the greenhouses are mostly unheated, as the climatic conditions allow the plants to grow perennially. This feature has a corresponding influence on the seasonal history of the parasites, which seems more or less to be identical to that in the field.

REFERENCES. 6, 10, 11, 21-3, 33, 64, 98, 99, 113, 125, 126, 128, 129, 145, 153, 158, 190, 203, 237, 264, 283, 290, 301, 330, 332-3, 335, 341-3, 347, 380, 417, 450, 497, 516, 525, 539-43, 560, 614-5, 616, 618, 633, 639, 651, 679, 689-93, 700, 702, 711, 753, 756, 762, 797, 799, 834, 854, 871, 889, 943, 946, 947, 964, 982, 985, 989, 990, 995, 996, 997, 1001, 1002-5, 1012, 1019-22, 1038, 1039, 1054, 1062, 1063, 1082, 1101, 1111, 1112, 1121, 1125, 1142, 1158, 1162, 1190, 1226, 1229, 1231, 1238, 1254, 1266, 1277-9, 1292, 1295, 1299, 1302, 1326, 1332.

Host Specificity

The research of host specificity of parasites undoubtedly represents a higher state of research. It must be based on a substantial level of taxonomic knowledge. Therefore, we can find various opinions on the host specificity of the group in the earliest records up to the present period. Some authors believed all the species to be strictly specialized species and each parasite reared from a distinct host species was described as a separate species. Nevertheless, it was soon found that the specificity of the group is wider and that the species are capable of attacking several hosts. Thus, an opinion on the wide polyphagy of the group appeared. Today's opinion of various authors, which is based on well-documented material, agrees in that we can recognize a number of various degrees of host range, from strictly specialized to rather widely specialized species among the aphidiids. However, differences in opinion on the factors that have determined the host specificity of the aphidiids still occur.

Host specificity is a rather important subject in the research of parasite biology. Without understanding the main features of parasite host specificity rather well we cannot understand a number of other problems, not to speak of applied themes.

~ HOST SPECIFICITY DEVELOPMENT. Two groups of opinions can be recognized generally as to the influence of a parasite on its host: one group of authors believes that the longer the host-parasite relation exists, the greater is the tolerance of the host to its parasite, and the less damage is caused to the host by the parasite. Evolutionarily younger parasites are believed to kill their hosts, while older species do not kill them. Contrary to this opinion, others believe that a parasite which kills its host is phylogenetically older or younger.

We feel ourselves to be rather far from being able to throw any generalization on the evaluation of host and parasite relations in the animal world. However, a certain comment seems to be necessary with respect to the host-parasite relations in aphidiids. The host group, the aphids, may be briefly characterized in this respect by manifesting three basic features: (1) the aphids produce a relatively rather high number of progeny, (2) their developmental cycle is relatively short, (3) their body size is minute. The parasitic group, the aphidiids, can be characterized as follows: (1) the whole group consists of aphid parasites exclusively, (2) each parasite requires a single aphid host for its development, its rate of development being longer than that of the host, (3) the

parasites are relatively large in size when compared with their hosts. It is apparent that it would be difficult for a parasite of the aphidiid group to feed inside a single host without severely influencing its existence as the food supply is too limited. This is one of the reasons, why the parasite kills its host. As to the evolutionary age of host and parasite relations, the following must be emphasized: it seems to be the principal function of aphid parasites to reduce the number of their hosts, which is advantageous for both sides: the host numbers are limited to a level compatible with the community equilibrium and food resources cannot be exhausted in consequence. The parasite can live because of host existence. Thus, the parasitized aphids must be killed otherwise the function of parasitism would be of no significance for the host as its population number would not be reduced. This viewpoint seems to be a basic one. Consequently, we believe that this relation between host and parasite is of a very ancient character.

Another aspect must be stressed with respect to host specificity development. The aphidiids are parasitic on aphids during their development, while the adults occur as free insects. Consequently, there are different requirements of a parasite species on the environment during its life. During its larval development, its requirements are determined by the host, otherwise the parasite larva could not survive; during the adult life, there is no dependence on host occurrence except for oviposition and food; the adult stage, therefore, is relatively free of the host. Consequently, as both the aphids and parasites are different groups of organisms, the requirements of parasite adults on the environment may be different from those of the aphids, while requirements of parasite larvae are conditioned by the host requirements. Therefore we have to stress that host specificity is a complex of requirements of adult parasite and its developmental stages.

As we will show in the chapter on phylogeny, the general evolutionary trend of aphids and parasites is the same: they originated in forest communities and have evolved to occur in conditions of drier environments. However, in details various differences in separate host and parasite groups can be recognized. Today, the number of aphid species is much higher than that of the parasites; a similar state obviously occurred in ancient periods. Apparently, the ancestors of the aphidiids exhibited a certain degree of host range, which allowed them to be relatively free as to selection of the most favourable environments, as they were not closely dependent on a single host species. Close host-parasite relations resulting in a strict host specificity are generally a regressive feature with respect to the whole group: if we compare the requirements of various recent aphid species that live in the same habitat, although they are more specialized than their ancestors, it is obvious that a wider host range of a parasite enabled it to occur in a given habitat irrespective of the detailed requirements of its host, consequently, the parallelism in host and parasite evolution was evidently true in certain, relatively few, specific cases.

— *Determining role of the main factors.* 1. Physical factors are original in the development of host specificity of parasites. Climatic changes and movements of continents resulted in the existence of certain climatic belts.

2. Floristic zones, habitats, communities. Suitable climatic conditions allowed the development of a rich plant cover. Corresponding floras developed in the different climatic zones, and were further differentiated by their changes. Rich floristic associations were followed by the evolution of phytophagous organisms, whose appearance was followed by the evolution of regulatory mechanisms—their natural enemies, predatory and parasitic groups.

3. Host. Aphids are a typical group of phytophagous insects that has evolved from the very early appearance of plants in ancient times (see. phylogeny).

4. Parasite. The parasite group became adapted as parasites of aphids as a conse-

quence of the regulatory mechanism of ancient communities; phytophagous hosts, their great numbers, and gaps in their limitation were naturally followed by an adaptation of a parasitic group as enemies of aphid ancestors. Today we know that this was not before the Adelgoid and Aphidoid groups of aphids were differentiated in the evolution.

Host specificity of a parasite is a result of the complex influence of all the factors, which may not be separated from each other as to their action as they are a unit, they condition each other, although they are different as to their significance with respect to separate cases. Their combined influence starts with physical factors, being followed by community, host organism and the parasite itself. Physical factors and the corresponding community present determine the type of habitat to which a parasite becomes attached, being followed by the influence of the host: host specificity is the result of the specific response of the parasite to all these factors. It must be classified on the basis of an evolutionary aspect.

We have shown the complex action and evolutionary aspect on parasite host specificity since our early studies on this subject (STARÝ 1959, 1964, etc.). Consequently, we must mention that the classification of our opinions as an "ecological theory" contrary to MACKAUER's "phylogenetic theory or application of Phylogenetic parallelism on the aphidiids" (see: MACKAUER 1963, 1965, etc.) is incorrect as we have already stressed the complex significance of habitat, host taxonomy and ecology, and parasite, for the host specificity, the degree of their significance being specifically dependent.

— HOST SPECIFICITY PHASES

— *Habitat finding.* Aphidiids are basically habitat dependent. Most of the species may be characterized by the occurrence in a defined type of habitat. Some of the species manifest less habitat dependence, but this is an exception, not a rule. Habitat preference is dependent both on horizontal and vertical zonation (see: distribution). The general type of habitat of a given species may be characterized by a certain floristic zone or its part, as has been clearly demonstrated in the distribution chapter. However, there occurs a further differentiation of parasite species inside these macrohabitats, due especially to different requirements of the species on the conditions of temperature and R.H. The well known examples of parasites of *Therioaphis trifolii* can be mentioned again: Although both the parasites, *Praon exoletum* and *Trioxys complanatus*, are members of the same faunistic complex and inhabit the steppe areas of the western Palearctic and attack the same host, they are very different as to their requirements on microhabitats. *Tr. complanatus* prefers drier and warmer areas, *Pr. exoletum* is restricted to less warm and more humid districts, both the parasites manifested the same requirements and corresponding distribution in the new environments in California (see: v.d. BOSCH et al., 1964, v.d. BOSCH 1957, etc.).

Consequently, we can characterize the phase of host habitat finding in such a way that the parasites occur in a defined type of habitat to which they are attached because of their specific requirements, and search for the host in the frame of this habitat. This is in agreement with the opinion of DOUTT (1959), who classified the host habitat finding as an initial and fundamental seeking of a certain environment by a parasite, irrespective of the presence or absence of the host. However, according to our opinion, it would be better to designate the first phase of host specificity as "habitat finding" instead of the "host habitat finding" of DOUTT, as the specific requirements of a parasite species to habitat are first, and finding the host in this habitat is a secondary question.

— *Host finding.* The second phase of host specificity includes the locating of the host in a given type of habitat.

The parasites generally seek for the hosts by flight or by running; the prevalence of either running or flight is specific, and is also conditioned by climatic conditions. The role of host microhabitat is of a different value: some parasites apparently search for a certain niche, such as curled leaves, gall, etc. *Ephedrus persicae*, for example, is a typical parasite of gall and leaf curling aphids in Europe. However, as mentioned by EVENHUIS (1964) it can attack also such hosts which are usually ignored, but when the latter are overpopulated and cause leaf-curling, the parasite may parasitize them (*Aphis pomi*, *Rhopalosiphum insertum*, etc.); the parasitization of *Aphis fabae* on *Euonymus europaea* by this parasite in Europe observed by us seems to exhibit the same feature. Similarly, the type of host colony may be important: a parasite may search for a free colony of the host, while it ignores the same host species colony in the same microhabitat if it is in a shady location: e.g. MCLEOD (1937) observed that *Myzus persicae* is attacked by *Ephedrus persicae* only on the more exposed parts of plants in a greenhouse, while *Aphidius matricariae* attacks aphids living in more shady situations; or another example may be mentioned on the basis of our observations: *Dacnusa rapae* when reared on *Myzus persicae* in a greenhouse, attacked only those individuals that lived on the flat leaves of Brassica plants, while aphids living in dense colonies on Asparagus stems were attacked only exceptionally; another example is that mentioned by GEORGE (1957) in *D. rapae*: the parasites preferred only *Brevicoryne brassicae* aphids on upper Brassica leaves, where the colonies were small and diffuse, while the colonies on middle and lower leaves were more dense and with a quantity of wax cover. Some parasite species are able to search for their hosts only when they are in great colonies, while the others are capable of finding even a single host specimen (Fig. 243). In more specialized parasites, the mode of host life plays a less important role and the parasites apparently seek just for the given host species, ignoring hosts that have a similar ecology: for example, we have observed that in semi-opened galls on *Populus* sp. caused by *Pachypappa* spp., both these aphids and also *Chaitophorus* aphids occurred; however, *Lysiphlebus satcaphis*, a specialized parasite of the *Chaitophorus* species, attacked only *Chaitophorus* aphids, although the niche was the very same for both species. Similarly, *Arctopron lepelleyi* attacks only the *Schizoneura* aphids living in galls on *Ulmus*, while galls of other aphids are left untouched.

The different role of host taxonomy and ecology may well be documented in this manner too. A number of other illustrative examples might be mentioned here.

The host plant does not seem to play any role in this respect. It may, however, cause another shape of the colony of the host aphid which the parasite avoids (see above). DUNITAN & CLARK (1938) mentioned preliminarily that the degree of parasitism of aphids on cotton depended on the degree of pilosity of cotton-leaves, they later found, however, that this had no significance and the aphid density was the main factor. The host plants of the aphids seems to have an influence in the host acceptance phase (see below). GRUBITSIS (1960) found that *Monoclonus crepidis* parasites exhibited a clear tendency to fly off the paper, whereas they remained on the piece of lettuce leaves which was the host plant of their host; similarly, there was a clear tendency to avoid various objects placed on a piece of paper, while a number of examinations were greater when the objects were put on the leaf, when, however, host aphids were used instead of inanimate objects, the results were less convincing. Statistical analysis has shown that different host plants had no influence on the degree of parasite attack on a given host aphid. Apparently, the parasites avoid the situations of places which are unfamiliar to them (piece of paper, etc.).

The mechanisms of locating the host individual seems to be a complex action of chemical, mechanical and visual stimuli. As the evidence shows, the relative significance of separate stimuli may be specifically dependent. SCHLINGER & HALL (1960)

- ◎ START POINT
 X END POINT
 ● APHID, APPARENTLY PARASITIZED
 ○ APHID, NOT PARASITIZED

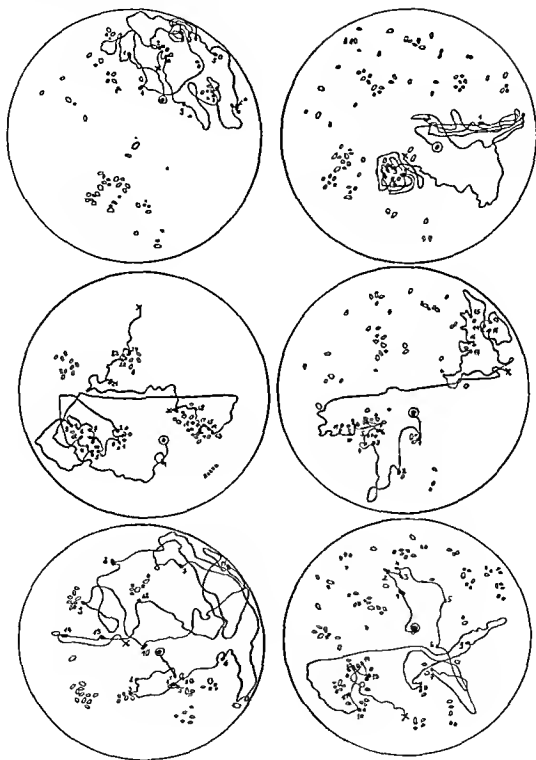


Fig. 243. Diagram showing movements of ♀ *Diacretella rapae* in colonies of *Brevicoryne brassicae*. Numbers indicate the sequence of apparently parasitized aphids (HAFEZ, 1961).

found that *Praon exoletum* was able to detect the aphid only by sensory control, at no time was it observed to be attracted directly to the aphid by odour or sight; however, some odour given off by the aphid and/or its honeydew are mentioned as a possible general attractant; when searching for a host, the parasite ♀ was observed to walk around, lightly tapping her antennae on the leaf surface in front of her and usually swinging her antennae from side to side. Chemotropic attraction is believed to have the greatest significance in locating the host in *Diacretiella rapae* by ULLYETT (1938). GRIFFITHS (1960) ascertained that both chemical properties of the host and sight participated in locating the host by *Monoctonus crepidis*, that a response to chemical properties of the host is important and was evidenced by the parasite's intent examination of the cast off skins of aphids, the empty flattened skins hardly resembling in shape the living aphids. However, attempts to alter the parasite host preference by smearing aphids with body juices of other aphids proved unsuccessful, possibly because extraction of the body fluids led to their being denatured in some way. The influence of sight on host selection was demonstrated by the following experiment: a parasite was attracted to and stopped to examine a dark spot or protuberance on a leaf surface. When unilateral illumination was used, the parasite stopped and examined the shadow cast by an aphid. When the aphids were separated from the parasite by a sheet of glass, chemical stimuli thus being excluded, the parasite stopped and examined the glass at the places where the aphids were underneath. As to the distance, relatively large objects, about 4 mm in diameter, were perceived from approximately 6 mm distance; smaller objects of 2.5–3.5 mm of diameter were perceived from about 3.5–4 mm distance and objects of approximately the same size as the aphids (1.0–2.0 mm) at a distance of 3–3.5 mm. The disregarding of chemical stimuli may be derived also from observation, where the parasites stopped and examined empty skins even when these had been empty for four years and apparently did not possess any chemical attraction.

– Host acceptance is a process which comes after the host has been located. It seems to be a very complicated process, where a number of factors come into play.

– Host species – It is a well known phenomenon in the parasites that are more widely specialized, i.e. where host range includes several host species, that these species of hosts are not attacked to the same degree by the parasite; some of them are obviously preferred, others are attacked less commonly. Such a situation may be found to occur in every species that has a wider host range. Nevertheless, a great number of samples must be used as a base for a similar classification of preferred species. SCHLINGER & HALL (1960) ascertained the following host preference of *Lysiphlebus testaceipes* in California: 1. *Aphis medicaginis*—excellent, 2. *Aphis pseudobrassicæ*—excellent, 3. *Aphis gossypii*—excellent, 4. *Rhopalosiphum maidis*—good, 5. *Aphis rumicis*—fair, 6. *Aphis helianthi*—poor, 7. *Myzus persicae*—poor.

A similar scheme can be found or elaborated on the basis of a more comprehensive study of aphid parasites of a given area (see e.g. STARÝ 1966).

Host preference can be influenced by a number of factors. If there is a lack of hosts in a given habitat, less suitable hosts may be attacked. Similarly, if there are suitable hosts and less suitable hosts mixed in a colony or they occur in a close neighbourhood, the oviposition activity of a parasite may cover the less suitable host species as well: SCHLINGER & HALL (1960) ascertained that *Aphis helianthi* and *Myzus persicae* are attacked by the above mentioned parasite when they are in the company of a more preferred host, *Aphis gossypii*. Similar conclusions were made by SEKHAR (1957) on the basis of his studies on *Praon aguti* and *Lysiphlebus testaceipes*. Similarity of host ecology has an influence also: according to EVENHUIS (1964), *Ephedrus persicae* attacked the overpopulated aphids, *Rhopalosiphum insertum* and *Aphis pomi*, because these overpopulated species caused leaf-curling of leaves in the same manner as the *Dysaphis*

aphids, the preferred hosts of the parasite. Host preference may or may not be connected with changes in actual fecundity; BROUSSAL (1966) found that *Diaeretiella rapae* exhibited the same fecundity when attacking *Brevicoryne brassicae* and *Myzus persicae* separately, although *Br. brassicae* was clearly preferred when both the species were mixed in equal numbers and occurred simultaneously. Host preference is also geographically dependent, it may exhibit quite different features in various parts of a parasite distribution area. The host plant may also have some significance. SEKHAR (1957) found that *Lysiphlebus testaceipes* preferred *Aphis gossypii* reared on melons in comparison with the same species reared on Hibiscus; similarly, *Myzus persicae* reared on the Nicotiana plant was preferred to the same species on other host plants. We have also observed some differences between the parasitization of *Aphis fabae* by *Trioxys angelicae* on *Euonymus europaea* and *Philadelphus coronarius* in Europe.

Host preference and factors influencing it is a rather complicated subject. It needs a detailed study, while we are probably only at the very beginning of its general research.

- Host density - If two or several host aphids occur in a single plot, usually one of the host species is preferred. PIMENTEL (1961) studied *Diaeretiella rapae* and its relation to *Brevicoryne brassicae*, *Lipaphis pseudobrassicae* and *Myzus persicae* on Brassica plants. The difference in the preference of one species for another was observed. However, density searching relationship is believed to play a role: if *D. rapae* is given an equal choice, it might prefer one aphid to another, but when one aphid species is abundant, opportunity for contact increased so that the more abundant species was the most parasitized. There seems to be no doubt that host species preference is an intrinsic phenomenon of a given parasite species or its population. Preference may become quite apparent when equal choice is given to a parasite. However, when there is a different abundance of species, the parasite attacks the most abundant one and consequently this species seems to be the preferred one; thus the community equilibrium determines the parasite preference. The actual preference between two or more species can be established only when an equal choice is given to a parasite.

This conclusion can be clearly demonstrated also by the experiments of BROUSSAL (1966), carried out on *D. rapae* and they complete the above mentioned observations of PIMENTEL very well. This author placed the same number of *Brevicoryne brassicae* and *Myzus persicae* aphids together and let 10 parasite ♀♀ oviposit freely under 20°C and 14 hour photoperiod. From a total of 4,975 eggs laid, only 268 eggs were deposited in *M. persicae* (5.4%). When only *M. persicae* was used under the same conditions, a total of 4,999 eggs were deposited in this aphid. Therefore, the preference of the parasite for *Brevicoryne brassicae* was well documented. HAFEZ (1961) received identical results.

- Host size - This in the frame of a host species seems to be equivalent to host instar preference (see: below). Host size with respect to separate species is a matter of host species preference (see above).

- Host instar - 1. Methods. Host instar preference can be recognized by two methods. The basic condition is that there must be sufficient specimens of all instars present and the environment must be suitable for the parasite (water, food, etc.). When using the first method, we leave a parasite ♀ to oviposit, then carefully collect all the aphids attacked, dissect them and so we can ascertain the percentage of separate instars attacked. The second method is a little more complicated. First, we let the aphid to oviposit gradually in a progeny of an aphid in such a way that all the instars are attacked; then we rear these parasitized aphids of various instars under identical conditions and determine the instar which is reached when the aphid is mummified; we are then able to derive the preferred instar from the corresponding

forms of aphids irrespective of whether they are apterous or alate. In most cases, it depends on the seasonal coincidence whether a given form is attacked or not. Several examples may be mentioned:

1. *Acyrtosiphon pisum*: *Aphidius ervi* in Europe occurs as early as the fundatrices in spring, and as late as the sexual progeny in the autumn; consequently, the fundatrices, parthenogenetic summer forms, and sexual autumnal forms are attacked by the parasite. This was proved also experimentally by us in the laboratory, where the parasites readily attacked both lower instar fundatrices as well as lower instars of summer parthenogenetic progeny and favourably developed in them.

2. *Aphis fabae*: On *Euonymus europaea*, the primary host plant, the aphid is attacked by *Trioxys angelicae*, *Praon abjectum* and *Ephedrus plagiator*. However, these parasites seem to occur later than the fundatrix in spring, so that they can attack only the progeny of parthenogenetic females. This parthenogenetic progeny later emigrates from the habitat and, consequently, the parasites which attack the aphid on its secondary host plants in another type of habitats, i.e. *Lysiphlebus fabarum* and *Lipolexis gracilis*, may attack only the parthenogenetic progeny. When the aphid immigrates to *Euonymus europaea* in the autumn, its parthenogenetic and later also sexual progeny is again attacked by the same parasite complex as in spring.

3. *Chromaphis juglandicola*: v.d. BOSCH, SCHLINGER & HAGEN (1962) observed *Trioxys pallidus* attack both parthenogenetic aphids in summer and oviparous progeny in the autumn.

In general, it seems that the fundatrices progeny that occurs in early spring is relatively less attacked by the parasites just owing to the lack of seasonal coincidence.

A somewhat different case is that of *Monoctonia pistariaecola*. This species obviously depends on the parasitization of the fundatrices of *Pemphigus* and *Forda* species, as these forms are on the one hand not closed inside a complete gall, on the other hand, they are of a relatively large size. In this case, the obligatory parasitism on fundatrix is apparently due to the phenomenon that the parthenogenetic progeny of the fundatrix is closed inside a gall, where the parasite is not capable of reaching it.

- Parasitized and non-parasitized hosts - Various opinions can be found in the literature as to the ability of parasite ♀♀ to distinguish between parasitized and non-parasitized hosts. A number of authors believe that the ovipositing ♀♀ are incapable of recognizing whether the host aphid had already been parasitized or not by the parasite ♀ herself or by another ♀: ULLYETT (1938)—*Diacretiella rapae*; WILBERT (1967)—*D. rapae*; HAFIZ (1961)—*D. rapae*; SEDLAG (1964)—*D. rapae*; SEDLAG (1964)—*D. rapae*; SCHLINGER & HALL (1961)—*Trioxys complanatus*. (However, FORCE & MESSENGER, 1964, found some tendency of avoidance). FORCE & MESSENGER (1965) found little tendency to avoid oviposition in hosts already parasitized in *Praon exoletum*.

Contrary to these opinions, SELJAK (1957) observed in *Lysiphlebus testaceipes* and *Praon aquii* a general avoidance of already parasitized aphids; ARTHUR (1944) made similar observations in *Aphidius? arenae*. LIDMANN (1924) even believed that *Trioxys angelicae* possesses sensory organs at the apex of ovipositor sheaths which serve to detect a parasitized aphid, as he found no case of superparasitism. However, SCHLINGER & HALL (1961) were right to doubt this opinion as no dissections to recognize superparasitism were made.

BROUSSAL (1966) divided the parasitized aphids into two categories before they were used in the experiments. *Diacretiella rapae* was unable to recognize already parasitized aphids in the case that they contained only parasite embryos, of a total number of 4,980 eggs 42.3% were deposited in the mentioned aphids. However, when the parasitized aphids containing parasite larvae were used, of a total number

of 3,849 eggs only 17% of the eggs were deposited in already parasitized hosts; therefore, in the latter case the parasite showed an incomplete discrimination ability. STARY (1962) observed a similar dependence in *Aphidius ervi*, where the parasite ♀♀ were able to distinguish the parasitized host in the case that it included higher instar larva or pupa of the parasite.

In our opinion, it seems that the parasites generally exhibit a rather low discrimination ability as to the parasitized and non-parasitized aphids. The avoidance of the parasitized aphids that contain a higher instar parasite larva seems to be due not to the presence of the higher instar larva, but to the fact that higher instar parasite larva usually occurs in a higher instar of its host, which in most cases is not preferred by the ovipositing ♀; consequently, the "distinguishing" between parasitized and non-parasitized aphids is due to host instar preference. There is no doubt that the degree of intensity of oviposition stimuli plays a role here as well; intensive oviposition stimuli force the parasite ♀ to try to oviposit even in aphid mummies, or in each other, etc.

– Live and dead hosts – Under normal conditions of host presence the parasite seems to pay little attention to dead hosts, especially if these have been dead for a longer time. GRIFFITHS (1960) killed host aphids of *Monoctonus crepidis* by freezing at a temperature of -9°C , the aphids were then left to warm up to room temperature; aphids killed 24 hours previously were less frequently attacked, aphids killed for 48 hours were not attacked at all.

– True and false hosts – Several observations were made on the influence of host aphid skins on the parasite oviposition behaviour. It was found in *Monoctonus crepidis* that the parasites examined the skins of their hosts, probably due to their chemical properties, although flattened aphid skins hardly resembled the living aphids in shape (GRIFFITHS, 1960). SEKHAR (1957) recognized that cast off skins of *Aphis gossypii* were examined by the parasites; rarely was the oviposition posture observed and no eggs were deposited; the stimulation due to cast skins gradually decreased and finally ceased altogether.

– Host behaviour – Parasites in general seem to be well adapted to a certain behaviour of the aphids which they exhibit when tapped by parasite ♀ antennae. Some aphids remain quiet; other species slightly move their legs or antennae; still others move their legs very strongly, pull their rostrum out of the plant and fall off the plant. If a parasite taps an aphid which shows a different response, the parasite is obviously discouraged and often breaks off oviposition attempts. The host behaviour is somewhat different in different instars, and is further influenced by temperature conditions, air movements, movements of plants, etc.

– Waxy coverings – A number of aphids have a more or less dense wax cover on their bodies. The parasites seem to be well specialized in oviposition behaviour in avoiding contact with this wax cover as they could severely injure themselves. The parasite behaviour is sometimes surprising, as for example, *Areopraon lepelleyi* emerges inside a semi-opened gall of *Schizoneura* aphid on *Ulmus*, which is full of honeydew and wax, and the parasite remains free of it. *Diaretetiella rapae*, a parasite typical of some wax producing aphids such as *Brevicoryne brassicae*, *Hayhurstia atriplicis*, etc., also restricts its attacks to those host individuals which are at the edges of the colony where the wax cover is not very developed, according to observations of GEORGE (1957).

Where this specific oviposition behaviour is lacking and the parasite oviposits under certain conditions in wax-covered aphids, the parasite gets injured. GRIFFITHS (1960) made laboratory experiments with *Monoctonus crepidis*, a common parasite of *Nasonovia* species, using other aphids as unnatural hosts to ascertain the influence of

Aphid Instar	Parasite ♀ No.										Total No.
	1	2	3	4	5	6	7	8	9	10	
III.	—	—	2	2	—	—	1	—	—	4	9
IV.	15	—	36	25	—	—	2	7	18	30	133
Adult	14	—	13	4	—	—	2	3	8	13	57
Total No.	29	—	51	31	—	—	5	10	26	47	199

20 aphids per ♀

Table 6. *Aphidius megourae*—*Megoura viciae*. Host instar preference and laboratory effectiveness (+ 10–14°C) as shown in mummified aphids (STARÝ, 1964).

Aphid Instar	Parasite ♀ No.										Total
	1	2	3	4	5	6	7	8	9	10	
III. No.	1	8	—	—	1	5	3	5	1	16	40
%	20	5.0	—	—	1.2	3.5	2.2	4.4	1.8	5.4	3.4
IV. No.	2	111	66	70	66	112	93	92	36	231	879
%	40	75	77	88	79.8	75	67.9	81.6	63	77	75.8
Adult No.	2	30	20	10	16	32	41	16	20	52	239
%	40	20	23	12	19	21.5	29.9	14	35.2	17.6	20.6
Total No.	5	149	86	80	83	149	137	113	57	299	1158

about 115
aphids per ♀

Table 7. *Aphidius megourae*—*Megoura viciae*. Host instar preference and laboratory effectiveness as shown in mummified aphids (+ 18–24°C) (STARÝ, 1964).

oviposition-mummification period in the separate instars. The latter method is very useful as it may be used for determining the host instar preference in field conditions when sufficient aphid mummies are at hand (see STARÝ, 1964).

2. Examples. *Aphidius avenae*: ARTHUR (1945), instar II and III preferred, oviposition in all instars. *Aphidius ervi*: STARÝ (1962), mummified instar III 4.8%, mummified instar IV 75%, mummified alate adults 7%, mummified apterous adults 15%. *Aphidius megourae*: STARÝ (1964) Tables 6–7. *Aphidius smithi*: WIACKOWSKI (1962), instar II and III preferred, followed by I and II, adults less frequently attacked. *Diaeretiella rapae*: BROUSSAL (1966), instar II and III preferred, but it may attack all the instars. SEDLAC (1959), middle size aphids preferred, but it may attack all the instars. HALEZ (1961)—similar results. *Ephedrus plagiator*: SKRIPSINSKY (1930), instar III and IV preferred in the laboratory, II and III in the field. *Praon* sp.: BODENHILMER ET NEUMARK (1955), instar I preferred. *Praon abjectum*: STARÝ (1966), higher instars preferred, I and II ignored or poorly attacked. *Praon exoletum*: SCHLINGER & HALL (1960), instar III and IV preferred, but all instars except the first were parasitized. *Praon volucre*: BEIRNE (1942), indiscriminate. *Trioxys angelicae*: STARÝ (1966), low instars preferred. *Trioxys complanatus*: SCHLINGER & HALL (1961), first three instars preferred, oviposition possible in all instars. *Trioxys indicus*: SUBRA RAO & SILARMA (1962). *Trioxys pallidus*: SCHLINGER, HAGEN & V. D. BOSCHI (1960), younger instar preferred, but oviposition in all instars.

3. Purpose of host instar preference. There is no doubt that host instar preference is quite intentional, it is not a matter of chance. Apparently, the most suitable instar for parasite development is selected, the composition of the body contents being favourable (glycogen, water, etc.). The size corresponds to the gradually greater developmental stages of the parasite, and the developmental period of the instar is long enough to enable the parasite to complete its development.

4. Influence of temperature. Experiments of STARÝ (1964) showed that temperature has no influence on host instar preference: *Aphidius megourae* exhibited the same preference both in conditions of $+10^{\circ}$ – 14°C and in $+18^{\circ}$ – 24°C (Tables 6–7).

5. Influence of intensity of oviposition stimuli. Host instar preference may be well observed and determined only in case that a ♀ is in the presence of its host relatively continuously. Host number must be sufficiently numerous, as well as all the instars being present. In case that a ♀ has not laid eggs for a longer period and then an oviposition chance is given to her, she does not distinguish the instars but attacks all the aphids she meets. This fact must be emphasized, as incorrect results could be obtained in observations where aphids of a given instar were put in a Petri dish and a parasite ♀ that had no chance to oviposit for a longer time is added, she may attack even adult aphids although generally preferring instars II and III.

6. Different reactions of separate aphid instars to parasite attack. Separate aphid instars reveal different reactions to parasite ♀ attack. If the aphid's response to parasite attack is generally negligible, there is consequently no difference. However, when the aphid shows a response such as movements of legs, etc., then it is a rule that these defensive responses are stronger in higher instars. Higher instars too, have longer legs and this can influence the result of parasite oviposition. On the contrary, it is difficult for the parasite's antennae to tap instars which are too small and which cannot, moreover, be successfully struck by the ovipositor.

7. Host instar preference and aphid dispersal. The parasitization, either intentional or facultative, of a higher aphid instar means that a parasitized aphid has reached an adult stage; it may even live for a certain time and produce a certain number of progeny. If the alate instars are attacked, the alate adult aphid may disperse and transport the parasite larva inside its body to a new environment. It is well known that in some species (*Praon exoletum*) this kind of dispersal is rather significant.

8. Morphological adaptations of parasites and host instar preference. The development of various accessory prongs in the genera *Trioxys*, *Bioxys* and *Metaphidius* is generally believed to restrict the oviposition ability of a parasite ♀ to a given host instar only. However, according to our observations, supported by those of SCHLINGER & HALL (1961) on *Trioxys complanatus*, or of SUBBA RAO & SHARMA (1962) on *Tr. indicus*, the *Trioxys* species are capable of attacking all the host instars, with of course a certain preference for a given instar. The accessory prongs and the whole apparatus, therefore, have apparently their principle function to hold the aphid and prevent its escape when the parasite tries to deposit an egg in it.

– Host form – The significance of a host's form can be considered from two aspects.

A. Apterous and alate forms. The preference of either alate or apterous forms by a parasite ♀ is caused by several reasons: In some aphids in a certain part of the season, only alate forms are produced so that the parasite cannot select an apterous form, this is the case of *Trioxys phyllaphidis*, a parasite of *Phyllaplys fagi*, and that of *Dyscratulus planiceps*, a parasite of *Drepanosiphum platanoides*. Both these parasites are known to mummify their aphid hosts in alate adult stage only. In other aphid species, alate progeny represents commonly a certain or even a total part of their progeny, either parthenogenetical or sexual; parasite ♀♀ do not basically distinguish apterous and alate aphids, and they prefer a certain host instar only; consequently, it depends on the relative number of alate progeny whether the percentage of parasitized alate adults is larger or smaller. For example, as mentioned by SCHLINGER & HALL (1960) *Praon exoletum* ♀♀ preferred second instar host aphids, both apterous and alate progeny being attacked.

B. Seasonal forms. The second group of aphid forms includes various seasonal

wax covers on an unadapted parasite: *Macrosiphum euphorbiae* from lettuce had a slight wax cover on its cuticle; the parasites appeared to spend extra time preening themselves after having come into contact with aphids or this species. *Brevicoryne brassicae* has also a strong wax cover; the parasite avoided the aphids, although rare attacks were also observed; after several minutes the parasites showed signs of damage, they fell on to their sides and backs and made vigorous attempts to rid themselves of the waxy film with which they had become contaminated by preening. This damage caused to the parasites is believed to be probably due to the oviposition behaviour of the parasite, which holds its legs on the aphid attacked when ovipositing.

- Host movements - In several parasite species we have observed that a ♀ remains in an expecting posture near a motionless aphid and oviposition follows in the case that the aphid moves a little. Other parasite species do not pay any attention to whether the aphid moves a little or not and oviposit in it. The latter case was experimentally proved by GRIFFITHS (1960): *Nasonovia ribis-nigri* aphids were anaesthetized by carbon dioxide and were offered in the presence of normal hosts to *Monoctonus crepidis* ♀♀; the parasites failed to distinguish between anaesthetized and normal aphids and readily attacked them.

- Oviposition stimuli - In the oviposition paragraph, we have shown that if an emerged ♀ does not have the possibility to lay its eggs, the oviposition stimuli gradually increase in intensity, and the ♀ is able to oviposit in aphids that would never be attacked if true hosts were present. Therefore, gradually increasing intensity of oviposition stimuli may overrule the other factors acting during the host acceptance process.

Intensity of oviposition stimuli in an ovipositing parasite gradually decreases to zero with age.

- Host suitability. If the stimuli determining host acceptance are suitable for the parasite ♀, she deposits an egg into the selected host. One would expect that after such a complicated process of host acceptance the egg would be deposited in a favourable host exclusively. However, as was correctly stated by BESS (1939), oviposition by a parasite is not necessarily an index to host suitability, the attractiveness of the host often being independent of its suitability for parasite development. This is quite true of the group of aphids as well. One can often observe that a parasite lays her eggs into hosts where the eggs either fail to develop or the parasite development is incomplete; this is often seen under both field and laboratory conditions. GRIFFITHS (1960), e.g. observed that *Monoctonus crepidis* oviposited in its true host, *Nasonovia ribis-nigri* on lettuce in the laboratory; the development of the parasite was complete. However, the parasite laid eggs to quite the same intensity in other aphids occurring on lettuce, such as *Aulacorthum solani*, *Macrosiphum euphorbiae*, *Myzus persicae*, *Neomyzus circumflexus*, although no development of the eggs was observed.

Similarly, under laboratory conditions, we can cause many aphids to attack unnatural hosts as well as deposit their eggs into them (see unnatural host propagation). BROUSSAL (1966), e.g., observed the attack and oviposition of *Diaeretiella rapae* into *Macrosiphoniella saubornii*, an unnatural host in the laboratory, but the larvae of the parasite did not develop past the third instar.

Under natural conditions, SCHLINGER & HALL (1960) found that *Lysiphlebus testaceipes* often attacks *Aphis spiraeicola* in California, although the parasite is not able to complete its development in this aphid and the larvae die before reaching the last instar larva stage.

This feature of parasite specificity seems to be a little strange, perhaps as a certain

incompleteness in a parasite species adaptation. However, it may be found to occur in the whole group, both in strictly and widely specialized species. It can, therefore, hardly be classified as a poor adaptation as it is highly improbable that a similar gap in adaptation would occur in the whole group. In our opinion, the difference between oviposition and host suitability for parasite development seems to be quite a rule, which allows a parasite to attack and oviposit in a greater quantity of hosts than in which it is able to develop completely. This feature may have a great significance in the host range of the parasite, as the parasite can perhaps find new hosts in this way, where its development is possible, and enlarge its range of specificity. If there would be a strict adaptation of a parasite in such a manner that only a strict number of favourable hosts would be attacked, no less suitable or new hosts met with in an environment would be attacked and thus would naturally cause an evolutionary regress in the parasite species. The trend to oviposit even in hosts that are not suitable for development seems to overrule even the strict specialization of various parasite species, where it is evident that no development will occur and the parasite is a relatively regressive species.

Consequently, because of this difference between oviposition and complete development, complete development of a parasite in a given host must be stated as a single correct criterium of host suitability.

— **HOST SPECIFICITY RANGE** is defined as a total of host species that are parasitized by an aphid parasite in nature. It is clear from this definition that the value of this range depends on our contemporary knowledge both of the distribution area of the species and of the number of hosts it attacks in this area. Gradually, as the research on the group is in progress, the classification of the range becomes more complete.

— **Actual and potential range.** The host range is basically determined by the distribution of the species. The distribution restricts the number of hosts which the parasite may attack. Consequently, we are able to recognize the actual host range of a parasite species. As it is known, each species is limited in its distribution by certain barriers. These barriers are of different kinds: geographical, biological, etc. Nevertheless, as it is also well known, there are a certain number of hosts over a barrier, which could be theoretically attacked by the parasite: such hosts are classified as potential hosts (see: host classification) and the parasite range as potential host range. When the barrier is crossed by the parasite species, these potential hosts fall within the actual range. The barrier can be crossed in different ways. Geographical barriers are crossed through the accidental or purposeful introduction of a parasite species into another country (across an ocean, etc.). Biological barriers may be crossed by changes in microhabitat conditions, seasonal occurrence, etc., the latter gives great possibility to laboratory work, where environment can be substantially controlled. Nevertheless, we must precisely distinguish laboratory and field conditions: A host accepted in the laboratory may be avoided in the field, as there the barriers occur.

— **Main types of range.** Several types of host range are distinguished among the aphid parasites.

Type 1: Host range is restricted to a single host species.

Examples: *Aphidius hortensis*—*Liosomaphis berberidis*; *Aphidius megourae*—*Megouraviciae*; *Aphidius phalaugomyzi*—*Phalaugomyzus oblongus*; *Aphidius ribis*—*Cryptomyzus ribis*; *Archaphidius greenideae*—*Greenidea ficicola*; *Dyscritulus planiceps*—*Drepanosiphum platanoideis*; *Lysaphidius schimitscheki*—*Liosomaphis abietina*; *Lysiphlebus fritzmuelleri*—*Aphis crataegi*; *Lysiphlebus horticornis*—*Metopencum fuscoviride*; *Monocotonus pseudoplatani*—*Drepanosiphum platanoideis*; *Pseudephedrus neotropicalis*—*Neolizerius* sp.; *Trioxys phyllaphidis*—*Phyllaphis fagi*; *Trioxys confusus*—*Greenidea ficicola*; *Trioxys cirsii*—*Drepanosiphum platanoideis*; *Trioxys pannonicus*—*Titanosiphon artemisiae*; many *Trioxys* species.

Type 2: Host range is restricted to two or more host species of the same genus.

Examples: *Aphidius absinthii*—*Macrosiphoniella* spp.; *Aphidius cingulatus*—*Pterocomma* spp.; *Aphidius fumebrus*—*Dactynotus* spp.; *Aphidius hieraciorum*—*Nasonovia* spp.; *Aphidius rosae*—*Macrosiphum* spp.; *Aphidius setiger*—*Periphyllus* spp.; *Aphidius areolatus*—*Periphyllus* spp.; *Aphidius sonchi*—*Hyperomyzus* spp.; *Diactetus leucopterus*—*Protolachnus* spp.; *Lysaphidus arvensis*—*Colorado* spp.; *Lysiphlebus salicaphis*—*Chaitophorus* spp.; *Monoclonus angustivalvus*—*Nasonovia* spp.; *Monoclonus crispus*—*Nasonovia* spp.; *Paesia* spp.—*Cinara* spp.; *Paesia unilachni*—*Schizolachnus* spp.; *Praon absinthii*—*Macrosiphoniella* spp.; *Praon bicolor*—*Protolachnus* spp.; *Praon pubescens*—*Nasonovia* spp.; *Praon silvestre*—*Periphyllus* spp.; *Praon exoletum*—*Therioaphis* spp.; *Protaphidius wissmanni*—*Stomaphis* spp.; *Trioxys aculephae*—*Aphis* spp.; *Trioxys falcatus*—*Periphyllus* spp.; *Trioxys complanatus*—*Therioaphis* spp.

Type 3: Host range is restricted to two or more genera of the same host group, more or less closely related. Other host groups are not parasitized.

Examples: *Aphidius transcaspicus*—*Hyalopterus*, *Longiunguis* spp.; *Aphidius tanacetarius*—*Metopcurum*, *Microsiphum* spp.; *Aphidius salicis*—*Cavariella*, *Sternaphis* spp.; *Areopraon lepelleyi*—*Schizoneura*, *Eriosoma* spp.; *Lysaphidus erysimi*—*Lipaphis*, *Pseudobrevicoryne* spp.; *Lysiphlebus arvicola*—*Sipha*, *Atheroides* spp.; *Praon abjectum*—*Aphis*, *Rhopalosiphum* spp.; *Praon flavinode*—deciduous forest Callaphididae (*Myzocallis*, *Tinocallis*, *Chionaphis*, *Eucallipterus*, *Tuberculoides* spp.); *Trioxys pallidus*—deciduous forest Callaphididae (*Myzocallis*, *Tinocallis*, *Chionaphis*, *Eucallipterus*, *Tuberculoides* spp.); *Trioxys centaureae*—*Dactynotus*, *Macrosiphoniella* spp.

Type 4: Host range is restricted to two or more genera of the same host group, more or less closely related. Other groups are rarely parasitized.

Examples: *Diactetella rapae*—main hosts: *Brevicoryne*, *Hayhurstia*, *Myzus* spp.; alternative hosts: *Brachycaudus*, *Sitobium*, *Schizaphis* spp.; *Ephedrus campestris*—main hosts: *Dactynotus*, *Macrosiphoniella* spp.; alternative host: *Megoura* spp.; *Praon dorsale*—main hosts: *Dactynotus* spp.; alternative hosts: *Acyrthosiphon*, *Megoura* spp.

Type 5: Host range includes several host genera of the same host group to which the main host also belongs, but few other host groups are attacked often. Mode of host life is important.

Examples: *Ephedrus uacheri*—main host: *Hayhurstia* spp.; alternative host: *Cryptosiphum* spp., both are leaf-curling aphids; *Lipolexis gracilis*—Aphidine and Myzine aphids; *Trioxys angelicae*—main hosts: *Aphis* spp., *Toxoptera* spp., alternative hosts: *Rhopalosiphum*, *Brachycaudus*, *Dysaphis* spp.

Type 6: Host range includes several or some host genera of various host groups. The mode of host life plays the most important role. Nevertheless, also in this type of host range a certain restriction takes place.

Examples: *Ephedrus persicae*—various leaf-curling aphids of Anuraphidine, Myzine and Aphidine groups; *Ephedrus plagiator*—various leaf curling and in dense colony living aphids (*Acyrthosiphon*, *Aphis*, *Brachycaudus*, *Ceruraphis*, *Dysaphis*, *Macrosiphum*, *Prociphilus*, *Schizoneura*, etc.); *Lysiphlebus fabarum*, *Lysiphlebus ambiguus*, *Lysiphlebus testaceipes*—many aphid groups, *Paralipis enervis*—root aphids (Pemphigidae—Fordinae, Eriosomatinae, Anoecidae, Aphididae—Anuraphidine aphids).

— *Width of range.* When the host range in the whole group of the aphidiids is classified it is obvious that a wider host range which restricts the parasite to a certain number of hosts is prevalent. Strict specialization and a rather wide specialization are less common.

When the separate genera are classified, then the following situation can be

ascertained: In monotypic genera we can find both strictly specialized (*Archaphidus*, *Pseudephedrus*) and less specialized (*Monoctonia*) genera. In genera including a low number of species there occur only less specialized species: *Aclitus* (2 species)—on root aphids; *Areopraon* (several species)—gall aphids; *Paralipsis* (2 species)—various root aphids; *Toxares* (2 species)—various arboricolous species, etc. In all the genera that include a great number of species we are able to recognize various types of host range, from strictly specialized to rather widely specialized species.

It seems that a relatively wide host range is more progressive. These species are ecologically more plastic, various races and strains can develop, which may result in the evolution of new species.

PHYLOGENETIC PARALLELISM RULE. The FAHRENHOLZ's rule or the Rule of phylogenetic parallelism or parallel evolution was published by this author in 1913, based on an examination of the host ranges of certain insect ectoparasites (*Anoplura*). MACKAUER (1961, 1962, etc.) applied this theory to entomophagous parasites, the aphidiids. He found that "host range of members of the Ichneumonoid family Aphidiidae (Hymenoptera) which are parasitoids of aphids (Homoptera: Aphidoidea) is restricted to units of their hosts that are taxonomically clearly defined". MACKAUER has further developed this theory (1965, etc.) applying it even as an aid to aphid classification. According to him, "there is reason to believe that aphids and their hymenopterous parasites represent a host-parasite association that possibly is unique in this respect" (1961, 1965).

FAHRENHOLZ's rule was criticized by many general parasitologists (PAVLOVSKIJ, etc.) especially because of its mechanistical viewpoint, which introduces artificial aspects into the evolution of host-parasite relations. Thus, it is only a surprise, that this rule that was so deeply criticized on the base of wide and well documented material of the animal world, has appeared in the entomophagous parasites, in the aphidiids. The whole trend of this book, as is apparent to the reader, clearly shows our basic disagreement and opposition to this rule. The reader can make the corresponding comparison for himself, as discussions are intentionally avoided in this book. For this reason, we have summarized our basic points of criticism as follows:

A parasite adult is a free insect, while its larval development is inside the host. The requirements of parasite adults, which are a result of a direct response of the adult to the environment, may be different from those of their larvae, as the latter are determined by the requirements of the host. We know cases where the parasite adults are unable to survive, although the aphid occurs unharmed in the same conditions.

Aphids exhibit parthenogenetic reproduction during favourable periods of the season, in the south it is the only type of aphid reproduction. The parasites are bisexual, uniparental reproduction being on a strain or population level, relatively rare.

The number of host species is considerably lower in the parasites than in the aphids. To cover their host group the parasites have developed generally a certain wide range of their host specificity, consequently, they often show greater ecological plasticity than their hosts, although they are basically habitat dependent in their occurrence.

In a part of the aphids in a temperate zone, obligatory host alternation has developed, connected mostly with habitat alternation. Nothing similar is known to occur in the aphidiids. The parasites are strictly habitat dependent: there are different complexes of parasites that attack the aphids in various types of habitats in which they occur because of host alternation, exceptions being rare. Parasites have generally adapted themselves to obligatory host alternation of aphids by (1) development of quiescent states, and (2) a wider host range.

A parasite may exhibit a different host range in various parts of its distribution area. We stress, in the original distribution area, not in the area that appeared due to accidental or purposeful introduction.

A host, better to say, a taxonomically defined host, is believed to be a basic factor in parasite evolution according to the Phylogenetic parallelism theory. This does not seem to be correct. A host is only a part of the parasite's environment, for example during a certain period of its lifetime (larval development). Host specificity starts with habitat finding, irrespective of a host's presence or absence, a host being found later in a given habitat. Parasite distribution may be derived primarily from various kinds of habitats (floristic zones), not from the host aphid distribution.

Taxonomy of the host is believed to be more important than host ecology, according to the Phylogenetic parallelism rule. In our opinion, taxonomy and ecology play a different part in individual cases. In some cases, taxonomy seems to be more significant, sometimes they are equivalent, sometimes ecology is prevalent. In every case, taxonomy and ecology, as well as the community, are the basic factors of host specificity development and in no case can they be considered separately.

Phylogenetic parallelism cannot explain why a given host species is attacked by different parasites in various parts of the world. If the evolution of host-parasite relations would be really a parallel, host and parasite distribution would be identical.

The phylogenetic parallelism rule supposes the responses of the host and parasite to the environment to be identical, parallel evolution being the result. This is an artificial aspect. Each group manifests its own responses to the environment. Naturally, the host is a part of the parasite environment and influences the parasite in a corresponding way. The phylogenetic parallelism rule ignores or cannot explain different responses of the host and parasite to the environment. Even MACKAUER considers certain features of parasite specificity as "secondary adaptation". We can only ask how a secondary adaptation is possible in case of parallel evolution? According to this rule, a parasite closely follows its host during the phylogeny. If secondary adaptation of parasites follows, they are a clear example that no parallel development of both the groups occurs.

One of the basic subjects of the Phylogenetic parallelism rule are the parasites of the aphids connected with Rosaceae. However, just this group of aphids represents a rare case of phylogenetic parallelism in aphids (higher taxonomic units).

The system of the aphid parasites cannot be mentioned as an aid to aphid classification. The system elaborated by MACKAUER has not been accepted by us as it is considered to be a very artificial one. We have restricted ourselves only to a more or less general separation of certain "groups", showing simultaneously how many characters are lacking which are necessary for an elaboration of a natural system.

We may conclude our criticism as follows:

1. The host specificity features in the Aphididae (Hymenoptera) do not differ basically from those of other groups of parasitic Hymenoptera, namely Ichneumonidae and Braconidae, where the host taxonomy and ecology is known to play a role of a specifically dependent value (see: TOWNES 1958, etc.).

2. In the aphidids, the rule of phylogenetic parallelism is applicable in some cases only; rarely applicable on a generic level, mostly only on a specific level. General application on the group is artificial, and it obscures only the existing host-parasite relations and their evolution.

- INTERSPECIFIC RELATIONS. Host specificity may influence the interspecific relations among the parasites. If we have a certain community, where several different aphid species occur, different situations appear because of different host range of separate parasite species present.

If the host range of the parasite species present is at least partially similar, there occur close interspecific relations among them: For example, *Aphis fabae* in the forest habitats in C. Europe is attacked by *Praon abjectum*, *Trioxys angelitae* and *Ephedrus plagiator*. Each of these parasites has its own host range, nevertheless, they come into interspecific relations because all of them attack the aphid mentioned, as the latter is one of the members of their host range; a similar situation occurs in the field, where the same aphids are attacked by *Lysiphlebus fabarum* and *Lipolexis gracilis*.

Contrary to the situation mentioned, situations occur where the host range of separate parasite species is basically different, consequently, there are no interspecific relations among them, although the following aphids and associated parasites are found in alfalfa fields in C. Europe: *Acyrtosiphon pisum*—*Aphidius ervi*, *Praon dorsale*; *Aphis craccivora*—*Lipolexis gracilis*, *Lysiphlebus fabarum*; *Therioaphis trifolii*—*Praon exoletum*.

— **PARASITE PROGENY.** It is a generally known fact that a parasite population which is reared from a host prefers this host as well when ovipositing. We have a comparatively small number of records at hand. There is no doubt that certain strains and races of parasites may be recognized in nature (see: intraspecific categories). The transferring of parasites from one host to another in the laboratory does not yield good results just due to the lack of parasite dispersal and sufficient preference possibility. It is apparent that the preference in the parasites is different for different hosts in various parasite species and no generalization is possible. A general picture on the host species preferences may be obtained when a great number of samples reared from various aphids of a given area is at hand. On this basis, it may become apparent that host specificity exhibits certain genetically fixed features and on this basis the experiments necessary may be undertaken.

— **LABORATORY AND FIELD.** Host species that do not fall within the host specificity range of a parasite species are separated by a certain barrier in nature. Natural conditions do not allow the crossing of this barrier, although the true relation of the host and parasite may be very close. Laboratory conditions permit us to control a number of factors in such a way that an aphid that is not attacked by a parasite in nature is attacked in the laboratory. Unnatural host propagation may show a considerable number of such cases, and their number is expected to increase when more intensive research on the subject is undertaken. Naturally, the barrier may be crossed in the laboratory only to a certain degree.

In most cases, laboratory results are usually not identical when the same relation of host and parasite occurs in the field. Nevertheless, we are at the very beginning of such studies. It is possible that when no preference possibility is given to the parasite (introduction), laboratory host-parasite relation will occur successfully in nature as well.

— **TAXONOMICAL RESEARCH.** Exact identification is a basic presumption of the research of host specificity of the aphidiids. Incorrect identifications mentioned in the earlier literature, before good revisions of separate aphidid groups were at hand, resulted in great difficulties when host specificity of separate species was dealt with. Consequently, it is advisable to start host specificity studies on a well determined material that was examined by a given author himself. Our recent trend is to revise the old records and gradually elaborate the separate faunas of the world (see: MACKAUER & STARY, 1967). Therefore, if fauna of an unknown territory is studied, host specificity problems may be elaborated as a second step, after the identification is made. Host specificity generalizations must be taken into consideration, as host specificity exhibits peculiarities due to geographic distribution so that different conditions may be found to occur in the area studied.

Many examples where incorrect identification was followed by incorrect ideas about the role of host specificity of separate species can be found in the literature.

The relation of a parasite species to its host represents an important part of its ecological characteristics. More and more identifications with host records added simultaneously represent better information on host specificity and on the given host species itself.

- *Aphid classification.* Aphids can be considered to be useless as an aid in the classification of higher taxonomic units of the plants. Close phylogenetic relations may be found only rarely, for example in the plant group Rosaceae and associated aphids. It is well known that aphids generally attack the plants irrespective of their phylogenetic age. Nevertheless, aphid specificity may be useful when smaller plant groups are classified.

Generally, a similar situation occurs in the aphidiid parasites. Close phylogenetic relationship may be found in some aphid groups only, such as the Lachnidae, Greenideidae, etc. Otherwise, the generic spectrum of the parasites is so dispersed over the whole Aphidoid group of aphids that we cannot recognize any developmental trends of the aphidiid genera and groups. Nevertheless, a different situation may be found on the specific level. The classification of host range in the whole group (see: above) has shown that certain groups of parasite species may be used to show certain relations that occur in their aphid groups. For example, parasites of the Daetynotine aphids can be mentioned (Europe):

Aphidius absinthii: *Macrosiphoniella* spp.

Aphidius fovealis: *Dactynotus* spp.

Aphidius phalangomyz: *Macrosiphoniella* (*Phalangomyzus* spp.)

Ephedrus campestris: *Macrosiphoniella*, *Dactynotus* spp.

Praon absinthii: *Macrosiphoniella* spp.

Praon dorsale: *Dactynotus* spp.

Trioxys centaureae: *Macrosiphoniella*, *Dactynotus* spp.

Trioxys pannonicus: *Titanosiphon* spp.

As these species of parasites attack the other aphid species to a lesser degree or not at all, they may be shown to support the aphidological classification.

Nevertheless, in other cases, ecology of the host group is prevalent in importance in the parasite specificity and obscures any taxonomic relations among the host groups. For example: *Ephedrus nachei* attacks both *Hayhurstia* and *Cryptosiphum* species. These aphids are of different taxonomic relations, but they are both leaf-curling aphids and the parasite specificity follows the host ecology. *Paralipsis enervis* attacks almost all the species of root aphids of several aphid groups with no taxonomic affinities. One could mention a number of such illustrative examples.

- *APHIDIO CONTROL.* 1. Introduction: alternative host problem. Alternative hosts in the new environments where a parasite species is introduced represent one of the problems of a parasite introduction program. If a parasite has no alternative host in the new environment, it may be strongly influenced by a temporary lack of its host, as it is unable to survive this period by parasitizing some of its alternative hosts. Widely specialized parasites are usually easier in this respect than the strictly specialized ones.

It seems that this is one of the biological control trends of the future to introduce really economically indifferent aphid hosts, which are alternative hosts of various parasite species, simultaneously or even independently with the introduction of aphidiid parasites. This could, at least in some cases, help the introduced parasites to survive the unfavourable period of temporary host absence. One example may be mentioned as an illustration: There is a monophagous aphid species widely dis-

tributed in S. Europe, *Longiunguis donacis*, which attacks the *Arundo donax* reed. This reed is common in waste places, irrigation ditches, and it seems rather to have more economic significance in households than to be a weed plant. The aphid mentioned is attacked by the following parasites in southern France according to SHARMA (1965): *Diaeretiella rapae*, *Lysiphlebus fabarum*, *Aphidius impressus*, *Lysiphlebus ambiguus*, *Aphidius transcaspicus* (author's note). We have found the same species to be infested by *Aphidius transcaspicus* in Italy. Thus, the aphid is a monophagous species, but it represents the host of a number of parasites that include many pest aphids in their host range. Consequently, it would seem advantageous to introduce the reed and the associated aphid, eventually the parasites as well, for biological control purposes. For example, *Arundo donax* occurs also in Cuba, but we did not find any aphids there.

2. Mass rearing: alternative and unnatural hosts. Alternative hosts of aphid parasites may be useful in mass-rearings of a parasite species in case that the main host aphid, the pest, is reared with some difficulty under mass-rearing conditions. Unnatural host exhibits the same features.

3. Parasite conservation. Host range of a parasite species is important also in an integrated control program. If a parasite species is a strictly specialized species, more care must be taken as no foci of this parasite would occur there where its host (pest) aphid would not occur simultaneously. In widely specific parasites the situation is somewhat better as they are capable of re-invading a territory in which they were temporarily eliminated e.g. by non-selective insecticide treatments, etc., as they attacked alternative hosts in the neighbourhood of the treated area.

REFERENCES. 19, 21-3, 24, 55, 60, 65, 80, 84, 98, 99, 114, 116, 129, 160, 162, 163, 183, 191, 194, 220, 224, 243, 274, 275, 290, 291, 294, 301, 304, 314, 342, 343, 345, 347, 356-7, 365, 376, 385, 396, 419, 421, 438, 445, 450, 470, 476, 478, 527, 535, 542, 549, 552-3, 556, 557, 614-5, 618, 645, 668, 679, 688, 689, 692, 693, 695, 696, 697, 700, 701, 703, 742, 705, 758, 776-8, 780, 782, 795, 837, 865-6, 867, 894, 895, 946, 949, 961, 963, 969, 973-4, 975, 979, 981, 982, 983, 984, 989, 995, 996, 1001, 1004, 1006, 1011, 1020-2, 1023-5, 1039, 1062, 1066, 1069, 1081, 1105, 1110, 1112-3, 1118, 1125, 1141, 1158, 1163, 1189, 1191, 1205, 1206, 1208, 1211, 1213, 1219, 1229-30, 1238, 1266, 1278-9, 1295, 1299, 1306, 1319, 1325, 1343.

Intraspecific Categories

The research of intraspecific categories in a given group of parasites is a higher degree of basic research, which may be based on a good level of taxonomical research. We have a relatively good knowledge of the aphidid fauna of certain restricted areas, or a good general idea about the fauna of wider territories, but the research of intraspecific categories needs a really good knowledge of a given species in the whole distribution area, and research of a given species should also be related to the whole group. Thus, our recent state may be characterized as an accidental establishment of the existence of certain biological races of parasites or at least of their indication. Research of intraspecific categories may consequently be classified as a subject of future research.

— SUBSPECIES is a geographically defined aggregate of local populations which differ taxonomically from other such subdivisions of the species (MAYR, LINSLEY & USINGER, 1953).

MAYR (1942) concluded, as a broad generalization, that the more sedentary a

species of animals is, the more it will tend to differentiate into geographical races. Consequently, it should be true that the more easily the individuals of a species are dispersed, the less diversification into geographic races takes place. The aphidiids are principally habitat dependent, being attached to a certain floristic zone. However, it is well known how the separate floristic zones overlap, and how the separate elements may be distributed: we may mention only the distribution of deciduous forest zone to the south due to its following of river valleys, etc. The dispersal of the aphidiids in a frame of a given zone may be high. Consequently, we are inclined to doubt whether we can separate any subspecies to occur among the aphidiids. According to our opinion, there will be apparently differences on a biological race level only. At least the subspecies described by MACKAUER (see: MACKAUER & STARY, 1967) in the aphidiids we consider as artificial: the examination of material of these "subspecies" has shown that they can be included in the variability range of a nominal form of a given species. They are: *Praon exoletum exoletum* (NEES) and *Praon exoletum palitans* MUESEBECK; *Trioxys angelicae angelicae* (HALIDAY), *Trioxys angelicae mediterraneus* MACKAUER, *Trioxys angelicae granatensis* QUILIS, etc.

- CLINES. A cline is defined as a series of adjacent populations in which the gradual and nearly continuous change of a character occurs. Differences in adjacent populations in clines may be ecological, morphological, physiological, etc. (MAYR, LINSLEY & USINGER, 1953).

Our knowledge does not allow us to distinguish any clines in the aphidiids for the time being. Perhaps, on a biological race level at least, we might distinguish various populations of *Lysiphlebus fabarum* in Europe, where it seems to be biparental in the North, deuterotokous in C. Europe (and C. Asia) and thelyotokous in Asia Minor, etc.

- BIOLOGICAL RACES. There are numerous indications showing the occurrence of biological races or strains to be common among the aphidiids. We can use several criteria to show the differences between various populations on an obviously biological race level:

1. Progeny. *Ephedrus persicae*. Uniparental thelyotokous in California and in Far East Asia; biparental in Europe and Canada (STARY & SCHLINGER, 1967).

Lysiphlebus desertorum. Uniparental thelyotokous in C. Asia, biparental populations unknown (STARY, 1965).

Lysiphlebus fabarum. Biparental in N. Europe, deuterotokous in C. Europe (STARY, 1966) and thelyotokous in Israel (ROSEN, 1967).

Lysiphlebus ambiguus. Biparental in C. Europe (STARY, 1966), uniparental thelyotokous in Israel (ROSEN, 1967).

2. Coloration. Dark and pale strains of *Trioxys complanatus* as a possible character of "strains" are mentioned by v.d. BOSCH (1957) from Iran. According to our observations, coloration changes in some species depending on the distribution area or on the seasonal period at a given area.

3. Host specificity. This seems to be the commonest case of differences on a biological race level in the aphidiids.

Diaretella rapae. It attacks, besides other aphids, *Brevicoryne brassicae* and *Myzus persicae*. According to GJORGE (1957) this species attacks *Br. brassicae* in England, but *M. persicae* is not attacked in the field, being parasitized only under laboratory greenhouse conditions. SIDLAG (1958) mentioned the degree of parasitization of *M. persicae* to be less in comparison with *Br. brassicae* in Germany. HATZL (1961) obtained similar results in the Netherlands. STARY (1966) gave records on the parasitization of both the aphids in the field in Czechoslovakia. BROUSSAL (1966) found experimentally that when *Br. brassicae* and *M. persicae* were mixed in equal numbers, the

former species was clearly preferred by the parasite; when *M. persicae* was isolated, the degree of parasitization was the same as in isolated *Br. brassicae*. PIMENTEL (1961) supported these observations by his independent results; moreover, relative density of separate species was found to influence the preference.

Lysiphlebus testaceipes. *Aphis spiraeicola*: Populations of the parasite occurring in California were not able to complete their development when parasitizing the aphids (SCHLINGER & HALL, 1960). STARÝ (1967) ascertained the populations occurring in Cuba to complete the development successfully. *Acyrtosiphon pisum*: This aphid is not attacked by the parasite in California, while heavy parasitization occurred in New Jersey (SCHLINGER & HALL, 1960).

Numerous cases of this type could be mentioned.

4. Temperature. According to SCHLINGER & HALL (1963) two races of *Aphidius matricariae* are distinguishable in California. Both the races are introduced, but one of them is restricted to greenhouses and their close neighbourhood and it is unable to survive in the open perennially.

5. Season. BROUSSAL (1966) recognized differences among the early spring and aestival generations of *Dicaetietella rapae* in France (fecundity, etc.).

6. Diapause. Obligatory diapause was recognized in *C. European* populations of *Ephedrus persicae* by STARÝ (1962), but it was not ascertained as occurring in the populations in the Netherlands (EVENHUIS, unpubl. suggestion).

- BIOLOGICAL CONTROL. Populations of a given parasite species may exhibit various biological features in various parts of the distribution area. With respect to progeny, thelytokous populations may be preferable for introduction. Similarly, temperature adaptation is important: when e.g. *Aphidius transcaspicus* was experimentally introduced into Czechoslovakia, there were three possibilities of selecting a population, either from the subtropics (Israel), where it occurs perennially; from Tashkent, C. Asia, where there are severe winters and hot summers; and from the Italian Riviera, where winter is not severe; in the two latter cases the parasite survives the winter in a quiescent state. With respect to the climatic zone to which Czechoslovakia belongs, the population from Tashkent would be preferable; technical reasons, however, do not often permit material to be obtained from the most suitable areas.

Evolutionary changes may occur when a species bridges a geographic barrier and colonizes a new region and so becomes widespread (ANDREWARTHA & BIRCH, 1954). An introduction means the simultaneous bridging of a barrier; consequently, we can expect that introduced species will gradually develop some features distinguishing them from their original populations in their home.

REFERENCES. 10, 116, 158, 196, 249, 275, 295, 497, 498, 565, 636, 688-9, 692, 693, 695, 696, 737, 741, 894, 895, 946, 953, 1000, 1004, 1006, 1019, 1123, 1125, 1127, 1130, 1134, 1207, 1208, 1210, 1213, 1309.

Effects of Parasitization on the Host

Parasitism is a complex historical process in which both host and parasite have played an active role. Nevertheless, host and parasite represent two different groups of organisms which show their own specific responses to the influences of environmental factors; parasitism is only a dynamic state which is a result of the pressure of the environment and vice versa, it has become an environmental factor that deeply influences both the participants of host-parasite relation; in other words, a phytophagous organism, the aphids, needed a regulation of their numbers by environ-

mental biotic factors in the frame of a community (natural enemies, including parasites) and, vice versa, parasitism has become a necessary part of the parasite life-cycle during the evolution of host-parasite relations. However, we must stress that in the latter case, the parasitic state in aphid parasites covers only a part of their life cycle, and, consequently, the parasites exhibit their specific responses to the influence of environmental factors either directly (adult stage) or through the responses of parasitized aphids.

It is well known that not every aphid species stays in a host-parasite relation with every species of parasite. Representatives of both groups have developed under the influence of governing factors of various communities; they have manifested various responses to these environmental factors which were similar or not to various degrees. This historical process has resulted in the present state where a parasite has a certain specific host range and, on the other hand, a host shows a certain selective power as to its parasitization by various parasite species.

There is a basic viewpoint on the host-parasite relation in that we must distinguish between the influence of parasitization on a host species (its populations) and the influence of parasitization on a host individual.

- **PARASITIZATION OF HOST SPECIES.** Natural enemies of insects have a great value for the host species in contribution to the relative stability of phytophagous insect populations, because they behave as—certainly imperfect—but somewhat density dependent regulatory agents (DOUTT, 1960). Thus, aphid parasites must be considered as valuable for the host species as they take part, being members of a natural enemy complex, in limiting the population of the host species in various communities and consequently preventing the destruction of a given food supply due to host population outbreak and elimination of the host species in a given community.

- *Group effect in aphids*

- **Parasitization** - BONNEMAISON (1948) recognized on the ground of field and laboratory observations that there is a distinct group effect developed in aphids. The gradually higher percentage of alate aphids in a colony is partially a result of this effect. Predators, as they consume a certain number of aphids, cause the decrease of aphid numbers in a colony and consequently a decrease of influence of the mentioned effect. However, according to our opinion, a different situation is to be found in parasites. Parasitized aphids remain mostly in a colony even as dead mummified aphids and therefore at least during a certain period, parasitization does not cause an immediate decrease of aphids in the colony, it may cause only a less rapid increase as the parasitized aphids do not usually reproduce. Thus, parasitization does not seem to have an apparent effect on the percentage of alate aphids in a colony through group effect. Naturally, we must eliminate such cases where the whole colony becomes mummified; usually, due to host instar preference by parasite ♀♀, a certain part of a colony remains unparasitized or the parasitization of aphid individuals in a colony is gradual so that both live and mummified aphids are found in the colony.

- **Intraspecific competition in aphids and parasitization** - WAY (1966) recognized experimentally that in aphid aggregations, even at a very early stage of aggregate formation, early instar mortality increases and fecundity of adults rapidly decreases: the quality of individual aphids also decreases as the aggregate grows. Aphid predators are mentioned as benefiting the aphids if they happen to remove sufficient individuals to decrease competition so that the remaining aphids develop into adults of better quality. Experiments have shown that the length of time before competition becomes important as a limiting factor is influenced by the size of the plant at the time of infestation, by the number of initial emigrants, and by the amount and rate

of growth of the plant including the extent to which damage by the aphids limits its growth; these factors modify the extent to which natural enemies influence the aphid population on the plant. There is a somewhat similar situation with respect to the parasites as in the above mentioned case. The parasites do not remove the infested aphids from the aggregation and do not consequently lower the degree of intraspecific competition in aphids.

– **Parasite dispersal** – As parasitization cannot influence basically the group effect in an aphid aggregation, it can maximally cause a somewhat slower increase of the aphid numbers during a shorter period. Therefore, an alate aphid formation follows. The latter state may cause either a gradual emigration of the aphids and the parasites that emerge later to disperse in the neighbourhood in search of other hosts; on the other hand, parasitized alate aphids can also serve as agents in passive transport of developmental stages of a parasite.

– **Dispersal of host and parasite.** PIMENTEL & AL-HAFIDH (1963) have shown that dispersal of the host follows natural enemy (parasite) action in experimental host-parasite populations: severe parasite pressure caused the host population to decline and eventually to break up into many small colonies. If at this time the environment provided adequate space, colonies tended to remain separated. Consequently, parasites must search more intensively to find smaller host colonies and they are forced to disperse more over the environment. With respect to the relation of group effect in aphids and parasitization, it is necessary to emphasize that in the case of PIMENTEL & AL-HAFIDH there was a long-termed action of parasites on host population and the parasite pressure was severe; these features obscure the influence of parasitization on the group effect in aphids.

– **PARASITIZATION OF HOST INDIVIDUAL.** A parasite, if it is to be useful for the host species as a limiting agent, must be capable of reducing a certain part of the host population in a given community. As a population consists of individuals, the parasite must be able to cause heavy injury to a certain part of host individuals. Thus, we may consider that there is a basic difference between a parasitization of a host species (population) and host species individuals: while parasitization is favourable for host species (population), it means heavy, lethal injury to a host individual. In other words, death of a certain number of host individuals due to parasitization is favourable to the existence of a host population in a given area.

– **Injury caused by separate developmental stages.** 1. Adult parasite ♀♀ cause direct injury by puncturing the host cuticle with their ovipositors and an indirect injury by depositing eggs into the host's body cavity.

2. Egg. The parasite egg obtains the necessary nutritive substances by an osmotic way. Otherwise, unhatched parasite eggs exert a juvenilizing effect on the parasitized host, producing metathetely (JOHNSON, 1959).

3. Larva. Instar I – III larvae feed osmotically. The newly hatched parasite larva diffuses into the host's haemolymph some cytolytic secretion, which visibly affects the young embryos and ova of the host, while ovaries, oocytes and pseudova are not changed: mature aphid embryos may survive and be laid by the aphid up to the period when the last instar larva starts its active feeding; this is the case of aphids parasitized in higher instar or in an adult stage (see: reproduction). Adipose tissue is attacked in a similar way (Fig. 244); as the parasite larva develops, the number of injured adipose cells correspondingly increases, until all the tissue in the aphids is involved. None of the important organs is injured during these stages of parasite development. Instar IV larva exhibits active feeding, it attacks all the organs and tissues of the host and finally kills it (SPENCER, 1926, ARTHUR 1944, MACKAUER 1959, TREMBLAY 1964, 1966, BROUSSAL & GAUMONT 1967). Parasite larva sometimes causes

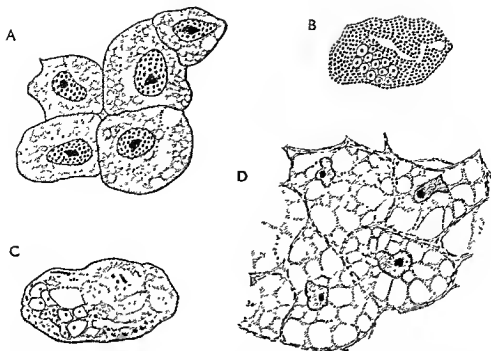


Fig. 244. Influence of parasitization on the host. A - normal adipose tissue of *Macrosiphum euphorbiae*. B - adipose tissue of *M. euphorbiae*, parasitized by *Praon simulans*. C - normal embryo of *Lipaphis pseudobrassicae*, sagittal section. D - embryo of *L. pseudobrassicae*, parasitized by *Diaeretiella rapae* (SPENCER, 1926).

the premature appearance of adult characters (prothetely) in parasitized aphids (JOHNSON, 1959).

An aphid is killed even if the larva is unable to complete its development inside a certain host (SCHLINGER & HALL, 1960, *Lysiphlebus testaceipes*-*Aphis spiraeicola* in California).

4. Prepupa and pupa occur inside or under the skin of dead mummified aphids, therefore, they cannot influence the host during its life.

- Influence on the host. 1. Development. Parasitization of aphids exhibits various influences on their developmental physiology when compared with the non-parasitized hosts. The first remarks on such differences seem to have been made by WEBSTER & PHILLIPS (1912) who recognized that the wings of *Schizaphis graminum* aphids parasitized later than in instar II are often imperfect. Detailed experiments based on *Lysaphidus platensis* and *Aphis craccivora* were undertaken by JOHNSON (1959, 1965). Apteriform nymphs parasitized in all stages continued their development normally without undergoing any major structural changes. Aphids parasitized in instar I were mummified in instar IV and a number of them showed some premature development of adult characters (prothetely) having the cauda intermediate in shape between nymphal and adult types, and patches of pigment on the abdomen and the lateral muscle sections. Aphids parasitized in instar II and subsequent instars developed to maturity and the only apparent external effect of parasitization in the resulting adults was suppression of pigment deposition on the dorsal surface of the abdomen and the retention of slightly juvenile pigmentation pattern of the head capsule.

Alatiform nymphs, parasitized in instar I were mummified in instar IV. At the time they died they had no alatiform structures, although the control series consisted almost entirely of normal alatiform nymphs. The parasitized nymphs were indistinguishable from normal unparasitized apteriform nymphs except that some of them showed some degree of prothetely. Thus in many of them, the lateral abdominal muscle attachments were pigmented and in a few there was a rudimentary, cleft genital plate, a cauda intermediate in size and shape between nymph and adult, and some pigmentation of the dorsal surface of the abdomen. Nymphs parasitized in instar IV were mostly mummified as adults and in adult stage they developed characters intermediate between alate and apterous, but in general appearance they were closer to the apterous form. All of them had rudimentary ocelli, and the antennal sensoria were either lacking, or when present, frequently very reduced in size and number. The degree of wing development varied: in some aphids there was no trace of pterothorax differentiation, in others the shoulders of the mesothorax were squared and small rudimentary wing evaginations were present. The head capsule was of the fully pigmented adult type and most of the aphids had some pigmentation of the dorsal surface of the abdomen. Aphids parasitized in instar III showed considerable variation in the extent to which alatiform structures were suppressed when they became adult. They all had ocelli, antennal sensoria and wing rudiments, but the size of the wing rudiments and the degree of differentiation of the pterothorax varied according to the time during the instar that the aphids were parasitized and the number of parasite eggs that were deposited in them. All aphids that were parasitized in instar II failed to develop pigment on the dorsal surface of the abdomen when they became adult, and most of them retained some of the nymphal pigmentation pattern of the head capsule. As to the differences, the aphids which were parasitized at the beginning of instar III all had smaller and more drooped wingpads than normal in the instar IV, whereas the wingpads of the aphids parasitized later in instar III were normal in the instar IV; in both cases the wingpads failed to differentiate much further at the final moult. Only in the superparasitized aphids was there any effect on the wingpads in instar IV; when they became adults, all the superparasitized aphids had small rudimentary wingpads. In aphids parasitized in instar IV, the effects on the structure of the adult cuticle caused by parasitization of instar IV nymphs were less marked than the effects of earlier parasitization; no matter how early in the instar IV they were parasitized or how many eggs were deposited in them, the aphids went on to develop distinctly alate structures, although these were sometimes imperfect. The earlier in the instar the aphids were parasitized, the more extensive were the effects of parasitization. Similarly as in case of instar III nymphs, superparasitism produced greater effects than single parasitism. Partial starvation, resulting in retarding the development of the host and thus enabling the parasite eggs to obtain a larger size before the host moulted, caused the increase of the effect of parasitization (JOHNSON, 1959).

The changes in host physiology due to parasitization were later (JOHNSON, 1965) recognized to be due to the premature breakdown of prothoracic glands in these aphids, which correspondingly influences the hormonal balance.

2. Rate of development. Detailed observations of various authors showed that parasitization has a significant influence on the rate of host development (HAFEZ 1961, STARY 1962, 1964, BROUSSAL 1966, etc.) (Fig. 245). Parasitization in separate instars has a different effect on the rate of host development: aphids parasitized in lower instars exhibit rather delayed development when compared with non-parasitized hosts, parasitization in higher instars exhibits less influence while parasitization in the adult stage hardly shows any difference.

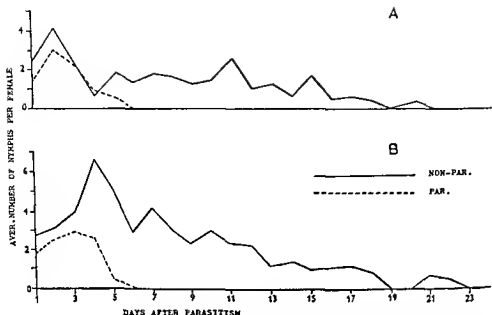


Fig. 245. Daily rate of reproduction of parasitized and non-parasitized *Brevicoryne brassicae*; parasitized as early adults. A – alate virginoparae, B – apterous virginoparae. Parasite: *Diactetiella rapae* (HAFEZ, 1961).

3. Behaviour. One group of aphid behaviour with respect to parasitization represents the reaction of aphids to parasite attack and oviposition. The mechanical reactions of the host against parasite attack were described in another paragraph (effects of host on the parasite, etc.). The response of the aphids to oviposition is various. Some of the aphids exude a small drop of yellowish or whitish fluid from the cornicles; this was observed in *Aphis fabae* parasitized by *Trioxys angelicae* (EIDMANN, 1924, STARÝ 1966) and in *Microlophium evansi* parasitized by *Aphidius ervi* (MACGILL 1923). Other aphids respond by quick movements of body or legs, other aphids remain more or less motionless, etc. Usually there remains a small drop of aphid haemolymph at the point where the ovipositor was inserted in the aphid body.

The second group of aphid behaviour includes the influence of the presence of developmental stages of parasite inside the host body. When lower instar larvae are present inside the host body, the behaviour of the aphid remains unchanged. When higher instar larva is present, the aphid manifests a gradually increasing sluggishness in movements. Just before the aphid is killed by the full grown larva, the aphid behaves in a peculiar way which is specifically dependent. In one group of aphids it remains in the colony and later becomes mummified. Examples: *Aphis fabae*, *A. craccivora* and their parasites; *Cinara bogdanowi* parasitized by *Praon abietis* and *Cinara piceae* (SCHEURER, 1964). In the second group the aphids in this state leave the colony and search and then remain at various peculiar situations where unparasitized aphids are rarely found. For example, *Acyrtosiphon pisum* parasitized by *Aphidius ervi* are found on the upper side of alfalfa leaves, or *Cinara pilicornis* parasitized by *Praon picta* and *P. picicollis* can be found at the tops of coniferous needles (SCHEURER, 1964). This typical behaviour of aphids which they show before being mummified may be considerably obscured by two circumstances: First, aphids of a given seasonal form behave in a certain way; they behave the same also when being parasitized, but it might seem that parasitization is responsible for this phenomenon. For example, v.d. BOSCH, SCHLINGER & HAGEN (1962) observed that *Chromaphis*

juglandicola parasitized by *Trioxys pallidus* could be found on the bark of trees in the autumn; but it was recognized that oviparous aphids seek primarily for woody parts of the trees to deposit their eggs in autumn irrespective of whether they are parasitized or not. We can confirm these observations by our own experience from C. Europe, where the mentioned aphids can be found on leaves in summer and on bark in the autumn irrespective of being parasitized or not. Second, an aphid colony may follow the growing parts of the plant and change its place on the plant, the mummified aphids are attached to the surface and after a certain period they may seem to have stayed there because of seeking a special situation before being mummified (*Macrosiphum rosae*—*Aphidius rosae*; *Dactynotus*—*Macrosiphoniella* spp. and their parasites, etc.).

4. Reproduction. Many authors observed that if the aphids are parasitized in lower instars, they are mummified before reaching maturity and thus they do not reproduce; when parasitized in higher instars or in adult stage they reach maturity and even reproduce for a certain period before being mummified (ULLYETT 1938, ARTHUR 1944, LIVSHIC 1946, BODENHEIMER & NEUMARK 1955, VIDANO 1959, HAFEZ 1961, STARÝ 1962, 1964, TREMBLAY 1964, SHARMA 1965, BROUSSAL 1966) (Fig. 245). Some records include even counts on the difference in the number of progeny of parasitized and non-parasitized aphids. Thus, LIVSHIC (1946) ascertained that *Aphis gossypii* parasitized by *Lysiphlebus fabarum* in instar IV produced 2.7 nymphs on an average after reaching adult stage, adults parasitized in adult stage produced 6 nymphs on the average before being mummified, when compared with the average production of 28.1 nymphs per a non-parasitized aphid. Similarly, SEDLAG (1959, 1964) found that *Myzus persicae* parasitized by *Diaeretiella rapae* produced 9 nymphs in comparison with the maximal number of 82 nymphs produced by non-parasitized hosts.

This influence of parasitization on host reproduction depends on host instar preference by the parasite ♀ (see: host specificity).

The action of various entomophagous parasites that attack adult insects and cause injury to their reproductive system is usually classified as parasitic castration. However, there is a different situation in the aphidiids as their developmental stages exhibit an influence on the larval to adult reproductive organs, but this is not a typical castration as only a part of the system is injured by the cytolytic action of the parasite larva and in cases of parasitized higher instar aphid nymphs or adults a part of the progeny may be produced successfully by the aphid. BROUSSAL (1966) correctly distinguished this feature in the parasitic castration caused by the aphidiids and proposed it to be classified as indirect parasitic castration; it may result in a partial or complete destruction of aphid progeny depending on the instar attacked, thus, it may be partial or imperfectly total.

5. Form of progeny. We have no data whether parasitization of an adult aphid, either in earlier instars or in adult stage, has an effect on the form of the aphid progeny produced by this individual.

6. Coloration. It is well known that mummified aphids are easily found and distinguished among the other aphids in a colony as they have a different colour; mummified aphids are black, brownish, yellowish and even whitish; partially, the relative age of the mummy may play a role in the intensity of coloration.

The coloration of mummified aphids is owing to two reasons: First, as ascertained by JOHNSON (1959, 1963) the coloration of aphid mummies may change in dependence on the host instar originally attacked as the parasitization of aphids in different instars can result in a various degree of prothetely and metathetely. *Aphis craccivora* parasitized by *Lysaphidus platensis* in instar I and mummified in instar IV exhibited

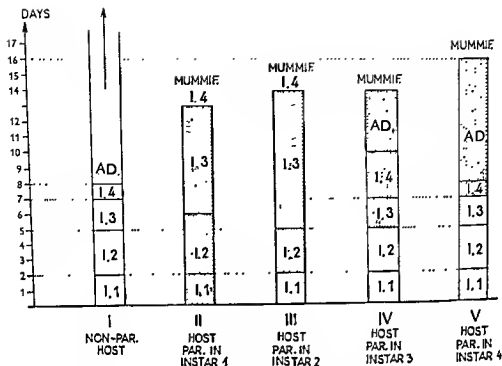


Fig. 246. Influence of *Diaeretiella rapae* on the development of *Brevicoryne brassicae*. (BROUSSAL, 1966).

some degree of prothetely—lateral abdominal muscle attachments were pigmented and there was also some pigmentation on the dorsal surface of the abdomen; aphids parasitized in instar II and mummified as adults had the head capsule fully pigmented, of adult type, and there was also mostly some pigmentation on the dorsal surface of the abdomen; aphids parasitized in instar III failed to develop pigment on the dorsal surface when becoming adult, and most of them retained some of the nymphal pigmentation pattern of the head capsule; the tergites of aphids parasitized in instar IV failed to become fully sclerotized and pigmented.

Second, the coloration of an aphid mummy is due to the secret produced from the silk glands of the last instar parasite larva. The silk production and gradual coloration of the mummified aphid due to cocoon spinning by the larva may well be observed at the early period after the larva has killed its host.

7. Shape and size. The mummified aphids can be distinguished from the other aphids in a colony also by their different size and shape. The latter phenomena are just a result of mummification. According to JOHNSON (1965), changes in endocuticle of parasitized aphids may be observed, the endocuticle becoming very much thicker than in normal aphids due to the influencing of prothoracic glands by the parasite. Moreover, a cocoon of a parasite is spun inside (or under) the dead parasitized aphid by the last instar parasite larva; in extreme cases, for example in some obligatory diapause cocoons (*Ephedrus persicae*) the mummified aphids may be rather remarkably different from the living aphids (see: seasonal history).

8. Longevity. Parasitization of an aphid causes a relative lengthening of periods of separate instars, but it generally means a shortening of aphid life in comparison with the non-parasitized host. This was observed by many authors (HAFEZ 1961, STARÝ 1964, TREMBLAY 1964, BROUSSAL 1966, etc. (Fig. 245, 246).

9. Dispersal. Whether a parasitized aphid is able to disperse or not depends on the host instar preference of the parasite ♀: if an aphid was parasitized in a lower instar, it may disperse over a plant as an apteriform or alatifform nymph; it is killed before reaching maturity and is not able to disperse off the plant as an alate adult. Aphids parasitized in higher instars or in adult stage may disperse over a plant as apteriform adults or off the plant as alate adults (see: dispersal).

10. Transmission of disease by parasites. Some entomophagous insect parasites are capable of transmitting a disease simultaneously with the insertion of the ovipositor. We have no information as to the aphidiid wasps in this respect.

11. Paralyzation of the host by parasite. The parasitic Hymenoptera may or may not paralyze or kill their hosts prior to oviposition (DOUET, 1959). We have shown in the oviposition paragraph that although the aphidiids apparently possess a poisonous gland, they do not seem to paralyze their hosts prior to oviposition in a certain way.

— CONTROL. In aphid control, we must distinguish between parasitization of a host species, a phenomenon which is favourable for the host, and parasitization of a host individual, that has lethal effects on the host individual. It is a basic problem in aphid control to establish the economic injury level of pest aphids. Consequently, it is important to know the level on which a pest may still be limited by the parasites (natural enemies).

It is important in the host-parasite relations that in most cases the parasitization of an aphid individual results in its death, a small part of its progeny being rarely produced.

REFERENCES. 21-2, 98, 106, 113, 129, 155, 158, 159, 186, 205, 211, 290, 291, 314, 438, 478, 591, 596, 597, 599, 644, 666, 681, 685, 857, 869, 890, 897, 954, 982, 996, 1003, 1005, 1019, 1022, 1024, 1029, 1039, 1062, 1101, 1111, 1121, 1125, 1162, 1231, 1238, 1254, 1256, 1266, 1278, 1285, 1319.

Effects of Host on the Parasite

As soon as the aphidiids have become adapted to parasitism on aphids the host has become a necessary part of their environment. A host represents the closest environment of developmental stages of the parasites. The parasite adults are not dependent on the presence of a host, but they must search for it to deposit their progeny and establish the existence of the species in the area.

— HOST AND PARASITE RELATIONS. A host is far from being a purely passive victim (SALT, 1941). It greatly participates in a favourable host-parasite relationship and favourable parasitism must be considered the result of the coexistence of host and parasite requirements in a given community. Two facts show the existence of such a relationship: on the one hand, a host species exhibits various defensive reactions to various parasites, on the other hand, a parasite species exhibits a certain host range.

— *Defensive reactions of aphids.* 1. Mechanical reactions. Aphids are known to exhibit various mechanical reactions as a response to parasite attack. For example, some aphids ignore entirely the presence of a parasite ♀ (*Aphis fabae*) and they show hardly any reaction when the parasite oviposits in them. Other species show feeble reaction to almost complete ignorance of the parasite ♀'s presence, sometimes moving their legs or even trying to escape (*Megoura viciae*). Other aphid species react very promptly to a parasite ♀ in pulling out their rostrum from the plant, running away and falling from the plant (*Microlophium evansi*—MACGILL, 1923, *Acyrthosiphon pisum*—STARÝ 1962, *Macrosiphum euphorbiae*—DUNN 1949). *Toxoptera aurantii* were observed to

start an upward spiral movement which is performed simultaneously by all the members of the colony in case of the proximity of a strange object (LARA & SHENEFELT, 1961).

Mechanical reactions of aphids are influenced by various factors. They change in dependence on temperature: aphids are more active and exhibit a higher degree of various reactions under optimal conditions, while low temperatures are responsible for their decrease. Similarly, rainy or windy weather may overrule the mechanical reactions of aphids to parasites as the aphids try to stay on the plant. Often rain and wind may be perhaps even typical of a certain zone, e.g. in Cuba where wind blows for most of the day and rain is common every day during the rainy season, we have observed aphid reactions to be generally lower. The reactions of the species can also change in dependence on the change of the mode of life: obligatory host alternating aphids may live, for example, as gall or root feeding aphids during a certain part of the season. Host instar is also of importance: in lower aphid instars the mechanical reactions are generally lower. Host form, either apterous or alate, can have a similar influence. In particular cases, as in *Drepanosiphum platanoides* (KENNEDY 1966) even the adult alate aphid behaviour may change according to the occurrence or lack of quiescent state.

2. Physiological reactions of the host may influence the developmental stages of a parasite inside the body of a living host. These may be negligible, in case that the host was infested by an adapted parasite. On the contrary, a host responds to the presence of a developmental stage of an unadapted parasite by encapsulation or similar reactions that are lethal to the parasite (see: unnatural host propagation).

Contrary to the mechanical reactions of the host which are influenced by the environmental factors to a various degree, the physiological defensive reactions are more constant.

3. Relation of the reactions. It seems that there is a certain complementary relation between the degree of mechanical and physiological reactions of the host: species that exhibit strong mechanical reactions have less effective physiological reactions, and vice versa. Mechanical reactions serve the aphid to defend itself against an attack of a parasite adult, while physiological reactions come in action when the mechanical reactions were unsuccessful; thus physiological reactions are second in action and have to injure developmental stages of an unsuitable parasite which were deposited through parasite oviposition in the aphid body. This is perhaps the case of WILBERT's (1967) experiments with unnatural host propagation: of the propagated unnatural hosts of *Diaeretiella rapae*, *Rhopalomyzus ascalonicus* showed feeble mechanical reactions, but strong physiological ones.

4. Parasite adaptation. Defensive reactions of a host species against parasite attack may be classified as a selection of a parasite species by this host as the reactions mentioned do not exhibit an influence on the adapted parasites, while they repel or cause injury to unadapted parasites to a various degree. According to our opinion, a host species exhibits such a selection because of the favourability of parasitization due to limitation of its numbers, on the other hand, it manifests a struggle for life in preventing the infestation by relatively too many parasite species which could be dangerous to the existence of the given species.

— DETERMINING ROLE OF THE COMMUNITY. Each community is a result of a shorter or longer evolutionary process. The same is true as to the relations among the members of this community. The governing mechanism of a community and historical factors have resulted in host aphid and parasite relations of today. Free gaps in the limitation of a host species have obviously played an important role in host-parasite relation. Consequently, we can classify the effect of the host on the parasite as a result

	Stage of host when parasitized	Rate of development of parasite ♀♀ (days)			Average body length of emerging ♀ in mm	Average no. of eggs in ovaries of emerging ♀
		From oviposition to mummification	From mummification to emergence of adult	Total rate of development from oviposition to emergence of adult		
I	Early I. nymphal instar	9.5	4.7	14.2	2.33	176
	Early II. nymphal instar	8.3	4.8	13.1	2.33	173
	Early III. nymphal apterous instar	7.6	4.7	12.3	2.39	197
	Early IV. nymphal apterous instar	7.5	4.3	11.8	2.40	203
	Newly moulted apterous adult	7.5	4.5	12.0	2.43	213
II	Early III. nymphal alate instar	12.4	7.7	20.1	2.2	216
	Early IV. nymphal alate instar	11.5	7.4	18.9	2.1	195
	Newly moulted alate adult	12.2	8.2	20.4	2.1	163

Table 8. Effect of stage of parasitized *Brevitryne brassicae* on the *Diaeretiella rapae* (HAFEZ, 1961). I = apterous II = alate.

of historically developed complex relationship of a host and parasite governed by a community.

— INFLUENCE OF HOST ON THE PARASITE. 1. Morphology. The host, as a part of the environment to which a parasite has become adapted, has shown an influence on the parasite morphology. The flexible abdomen of a parasite ♀ is an apparent functional adaptation that is general for the whole group of parasites. Besides, we can distinguish various shapes and sizes of ovipositor and ovipositor sheaths. In some species, even accessory apparatus has developed to enable a more successful attack on a host (*Trioxys*, *Bioxys*, *Metaphidius*); the tubuliform shape of abdomen in *Protopholidius* is a similar adaptation.

2. Rate of development. A host species does not seem to have an influence on the rate of parasite development. Nevertheless, according to TELENGA (1950) it is believed to be host-dependent: rate of development of *Lysiphlebus fabarum* was 6–8 days in *Aphis craccivora*, but 7–10 days in *Brachycaudus cardui* under the same conditions. The latter data must be revised as it is possible that the parasite species includes two species ("*Aphidius cardui* MARSHALL").

Certain differences in the influence of different host instars on the corresponding rate of parasite development were ascertained by HAFEZ (1961) in *Diaeretiella rapae*: the total rate of development was found to be slightly longer in parasitized instar I and II aphids (Table 8). Similarly, certain differences were found between parasitized apterous and alate aphids, the parasitized alate hosts causing a longer rate of parasite development. Observations of BROUSSAL (1966) support these results.

3. Size. The influence of a host species on the size of a parasite is apparent when we compare specimens of a given species reared from various aphid hosts: e.g., we have reared *Ephedrus plagiator* from *Prociphilus fraxini* field samples in the laboratory and the emerged adults were rather large in size; this living adult material was transferred to another cage to parasitize *Aphis traccivora* and the parasite progeny obtained was extraordinarily small. This may be well understood from the comparison of the body size of the hosts.

Host instar also influences the body size of parasite adults. HAFEZ (1961) (Table 8) recognized apparent differences between adults of *Diaeretiella rapae* reared from various host instars in the laboratory. Moreover, he also found differences between apterous and alate hosts (Table 8). STARÝ (1964) obtained similar results in *Aphidius megourae*: parasites reared from aphids that were attacked in instar I and reached instar III when being mummified were distinctly smaller than those reared from aphids parasitized in instars II, III, IV and adult stage, respectively.

4. Sex ratio. Host species does not apparently have an influence on the sex ratio of parasites (STARÝ, 1964) of aphids.

5. Behaviour. Each parasite species exhibits a typical specifically dependent behaviour. This can be seen from the comparison of various types of parasite behaviour. This behaviour becomes untypical when an unfavourable host is met with as the mechanical responses of the host are not those expected by the parasites (see: oviposition).

6. Fecundity of a parasite seems to be influenced by a host species through the influence of host on the size of the parasite. HAFEZ (1961) recognized influences of the parasitization in various aphid instars on the number of ovarian eggs in parasite ♀♀: the number of eggs was lowest in parasites reared from aphids parasitized in instar I and highest in parasites reared from aphids parasitized in an adult stage; this is interesting as the parasite usually prefers II - III instar aphids (Table 8); nevertheless, HARTZ obtained opposite results in the progeny of parasites reared from parasitized alate aphid nymphs.

7. Longevity. As we have mentioned in the longevity paragraph, the parasite adult longevity may increase in dependence on the presence of adult food. As a host is a producer of honeydew which is the food of parasite adults, it consequently influences the longevity of adult parasites too.

8. Life history. The main peculiarities in the aphid life-cycle, i.e. the adaptation to unfavourable conditions through migration (host alternation) and quiescence have deeply influenced the parasite seasonal adaptation. Some parasites have developed a wider host range, other developed corresponding quiescent states (see: seasonal history).

9. Dispersal. Parasitized aphids may live inside a colony before and even after being mummified by a parasite, or they leave the colony and may move to other parts of the plant. Parasitization of higher instar alate nymphs to adults results in a passive dispersal of parasite developmental stages to other places through aphid migration.

10. Population density. Density dependence in host-parasite relations may be important for the increase and decrease of parasite population numbers.

11. Defensive significance of some phenomena in aphid biology. We find somewhat different opinions in literature as to the significance of some phenomena in aphid biology with respect to parasites. Earlier authors for example considered many features of aphid biology to be of an obviously defensive character. NEVSKY (1929) can be mentioned as a representative of these authors. According to our opinion, these ideas were due to an incorrect viewpoint applied to host-parasite relationship

in such a way that parasitism was classified as a phenomenon unfavourable to the host, the latter trying to develop defensory reactions and adaptations against parasites in general. As we have already mentioned, parasitism today is accepted as a phenomenon that is favourable for the host in limiting its numbers. There are, however, many defensive reactions against parasite attack developed in the host; this is due to regulation of the number of parasite species while there are no defensive reactions against adapted parasite action.

High reproductive potential and short rate of development are usually considered to be the most important defensive feature of aphids against natural enemy action (see also MACKAUER, 1959). In our opinion, the mentioned features of aphid biology are due to a combination of intrinsic features of aphids and favourable conditions of the environment; the action of parasites (natural enemies) is due to limiting the aphid number to a certain level determined by the community equilibrium.

Aphid migration. As we have shown (see: seasonal history) aphid migration cannot be classified as due to the escape of parasite action.

The ability of aphids to cause galls and to live inside those galls does not protect them from the action of parasite species either. Gall producing aphids are attacked by many parasite species which reveal various degrees of adaptation.

Wax covers are unfavourable for parasites to a various degree; adapted species of parasites attack aphid species that show poor or rather strong wax covers.

The covering of plants by honeydew is far from being a defense against parasite (natural enemy) action. Honeydew seems to act as an attractant for parasite adults, as it supplies food for them. Heavy honeydew cover occurs in aphid colonies mostly at their decrease, parasites usually having deposited their eggs earlier in the colony; this can be commonly observed in nature. Moreover, a heavy cover of honeydew is a favourable substrate for various aphidophagous fungi under certain conditions.

The sprinkling of honeydew does not seem to have an influence on parasite attack as the parasite adults attack the aphids from different sides.

The jumping of aphids does not mean an escape from parasite action either. We know a number of parasite species that are specialized in attacking just these aphids.

Flattened shape of aphid body: practically, all the aphid groups that exhibit various degrees of flattening the body are attacked by the aphidids, with the exception of an extreme case, *Cerataphis* sp. However, even in the latter case, the aphids are attacked by another group of parasites.

Dispersal. The dispersal of aphids over a plant or area may or may not prevent the aphids from being parasitized. In some parasites it may mean a temporary escape from parasite action, as they are not able to find small or middle-sized aphid colonies. Other parasite species may find even highly dispersed hosts as they have a strong searching capacity.

— CONTROL. A corresponding viewpoint must be applied also in aphid control principles. A host must be considered as a necessary part of parasite environment; the dependence of parasite on the host is different in various stages of parasite life. A host exhibits an active influence on the parasite as well. The effect of host on the parasite is the result of a historically developed complex relationship of a host and parasite governed by a community.

REFERENCES. 20, 21-2, 165, 198, 282, 290, 301, 339, 353, 365, 367, 376, 421, 476-8, 614, 615, 618, 650, 657, 679, 681, 685, 817, 854, 872, 964-72, 975, 1037, 1077, 1101, 1111, 1121, 1125, 1162, 1189, 1229, 1276, 1304-6.

Parasite Adaptation

The development of parasite adaptation is a rather slow and long process. It started at the period when the ancestors of the recent aphidiids began to adapt themselves to parasitism on aphids. Today's features of the parasite adaptation as a whole are a dynamic result of this process. During this process, the host has become a necessary part of parasite environment during a certain period of the parasite's life. Consequently, the parasite is much more dependent on the occurrence of the host than vice versa: a parasite needs obligatorily a host, while a host may be limited in its numbers by other natural enemies that can replace each other in action. Naturally, this is the basic schematical relationship. The evolution of host range of a parasite has enabled the parasite to be dependent on a host, but this host may be represented by several host species.

The aphidiids, being typical parasitoids, are attached to the host during a certain period of their life. A laid egg and larva are fully dependent on the host's presence, thus dependence is less in prepupa and pupa, while the adult occurs as a free insect, although it is attached to the host through oviposition possibility. These factors in parasite biology have exerted a basic influence on parasite adaptation. The adult stage is the most important as the parasite cannot survive in such an environment, where it can develop in an aphid but cannot occur as an adult; thus the requirements of the parasite adult are the most typical for the parasite species of population, while the general requirements of a parasite species may be partially obscured by the influence of the host. We must stress that a host is a part of the parasite environment and of secondary significance with respect to the adult stage of a parasite. A parasite adult is first influenced and must exhibit an adaptation to the abiotic influences of the environment; only after such adaptation has developed, the parasite is capable of surviving in a given environment successfully. Naturally, we cannot separate both these processes in nature, i.e. the adaptation of a parasite to abiotic environment and adaptation to the host as a part of the biotic environment, as these processes are complex in action. However, just here we can recognize the specific differences between the host and the parasite as separate organisms. The same environmental conditions influence the host and the parasite to a different degree, consequently, the host and parasite may not be equal as to their distribution. A great number of cases could be mentioned as a proof of this: we can often find in nature that the host and parasite exhibit various distribution areas (see: Distribution). Strictly specialized parasites, generally, exhibit a closer adaptation to the requirements of the host, while a wider host range enables the parasites to cover even a greater distribution area than that of the host.

— **PARASITE ADAPTATION IN SEPARATE DEVELOPMENTAL STAGES.** A laid egg and larval instars live inside the host's body. They cannot occur outside a host and thus they show the greatest degree of adaptation. Decreased size of eggs as well as the reduction or absence of the yolk are apparent adaptations due to parasitic life. Similarly, the larvae are adapted to the parasitic life both as to their shape, respiration, excretion, and manner of feeding. The prepupa and pupa exhibit less dependence on the host. They occur inside or underneath the host body skin inside a cocoon that was spun by the last instar larvae. The adult parasite is a free insect and has no direct dependence on a host at all. However, a host's honeydew is the food of the parasite adults. Further, the parasite adult ♀ must find the host and deposit her eggs inside the host's body to secure the existence of the species. consequently, various adaptation in host specificity and oviposition behaviour can be found in parasite ♀♀.

— **KINDS OF PARASITE ADAPTATION.** Parasite adaptations to the host may be recognized in many features of parasite biology. They are separated into the three following

groups altogether, all of them are, to a certain extent, connected with each other. We have dealt with the adaptations only schematically here as they are mentioned in separate paragraphs in more detail.

— *Morphological adaptation.* These adaptations are best seen in the parasite adult ♀♀. A flexible abdomen, shape of first abdominal tergite, shape of abdomen, shape of the ovipositor sheaths and even the accessory prongs enable the ♀ to attack the host more successfully. Sexual differences resulted also in morphological differences in the shape of the abdomen of ♀♀ and ♂♂, respectively. A parasite egg may temporarily change its shape when deposited, as the diameter of the ovipositor is less than that of the egg.

The shape of the parasite larvae of different instars is an adaptation to a gradually more restricted space inside the host's body; the first instar larvae are much less arcuate in shape than the final instar larvae, as the latter are rather large and finally cover the whole inside of the host's body.

— *Ecological adaptation.* Practically, all the factors that influence the host specificity of the parasite may be classified as an adaptation of an ecological kind, an adaptation to the environment as a whole and adaptation to the host as a part of this environment. While the first phase (habitat finding) of the host specificity process is not dependent on the host, further phases are partially an adaptation to the host: a parasite must be capable of finding its host in a favourable microenvironment, of occurring in a favourable period and of developing such adaptation that would allow it to survive the period when the host is absent. Then, oviposition behaviour is a result of a strong adaptation of a parasite to the host.

— *Physiological adaptation.* Generally, a parasite must adapt itself to the environment of the host's body in two main directions: First, it must be immune to the influences due to the host's organism; immunity is a result of a rather long and slow process in nature. Second, it must feed on the host in such a way as to not cause injury to the host's vital tissues earlier than before it has finished its larval development.

REFERENCES. 161, 166, 211, 247, 290, 688, 701, 719, 954, 1003, 1005, 1111, 1121, 1125, 1163, 1219.

Host Adaptation

Various opinions occur on the host-parasite relationship and the role of the host in this connection: on the one hand, the host is believed to be the passive victim of the parasite, on the other hand, the host is believed to exhibit an adaptation to enable the attack of a given parasite. As to the latter case, for example BURNETT (1949) believes that host and parasite show mutual adaptation for the preservation of the system (see: DOUTT 1959). Similarly, TING, HOLDAWAY & CHIANG (1966) classify parasitic relation established in nature as involving both ecological and physiological adaptation between the host and the parasite: on the part of the host, there is a lack of immunological reactions and adequate nutritional supply.

We have mentioned earlier that DOUTT correctly classified parasitism to be useful for the host as well, as it means the limitation of host numbers, thus preventing overpopulation and heavy injury to the basic food supply of the host. However, in our opinion, there is no doubt that parasite adaptation is much closer than that of the host: an aphid parasite cannot occur in nature without the presence of its host, the host, however, is capable of doing so. We believe that a host species does not adapt itself to a given parasite species, but exhibits specific and active selective ability that enables it to allow only a certain number of parasite species to attack it and partially reduce

its population in a given community. Thus defensive reactions (mechanical, physiological) in a host do not seem to be an adaptation to the parasite, but a result of specific features of the host to which a certain parasite had to adapt itself. A host seems to exhibit the same mechanical defence against all the parasite species if their ♀♀ attack it, but some of the parasite species have become well adapted and may attack such a host successfully; the same is apparently true as to the physiological reactions.

We have observed that a given host species may or may not be attacked by parasites in various communities. Physiological and ecological features of the host mean that it is attacked in a community by a number of natural enemies, which replace each other in action, the community equilibrium being the governing mechanism. Thus it is apparent that to occur as a member in a given community a given host species allows a certain natural enemy (parasite) species to attack it and to reduce its population numbers. As host-parasite relation is important for both the participants, they try to preserve the system: the selection of the parasite seems to be the question of the host and parasite relations, the degree of parasite attack is determined by the community. The parasites are basically habitat dependent and their dependence on the given host is various; they may attack several host species in this habitat and in such a case they are not strictly dependent on the occurrence of one of these host species in a community, or they may be strictly specialized and then are dependent and adapted to the life history of the host to a high degree (see: seasonal history, host specificity).

REFERENCES. 166, 290, 615, 954, 1219.

Host Classification

With respect to host-parasite relations the host aphids can be classified from different points of view.

— *Host preference.* 1. Main host. It is clearly preferred by the parasite in a given geographic area.

2. Alternative or subsidiary host. Such a host is parasitized occasionally, to a lesser degree than the main host in a given geographic area.

3. Facultative host. It is parasitized only exceptionally.

Extensive material of samples from a given area must be taken into consideration before such a host differentiation is made with respect to a parasite species in the given area. Moreover, there can be geographic and seasonal variation.

— *State of host-parasite relationship.* Generally, certain hosts are known to be attacked by certain parasite species in a given area. Such a state occurs in nature, it is a fact, so that such a host has to be called a "factitious host". Nevertheless, there is another case, when another host species exhibits almost identical features as the factitious host; however, due to geographic or other barriers, the given parasite species is unable to parasitize the aphid mentioned, although there exists the theoretical possibility of such a relationship. This host, therefore, must be called "potential host" (PAVLOVSKIJ, 1946).

The above mentioned classification is rather important for a parasite introduction program when planning the introduction of separate species with respect to the faunistic complexes of parasites and the occurrence of pest aphid species controlled; vicariancy is a rather apparent example.

— *Host parasite relationship in phylogeny.* In some cases of apparently close host-parasite relationship, we may classify a certain host aphid as a "phylogenetical host" of a parasite species. Naturally, such a viewpoint must be understood in a dynamic

way; all the host species are undoubtedly also phylogenetical hosts as all of them played a role in the evolution of a parasite species, although such a role was of a smaller or greater significance. The term "phylogenetical host" is perhaps better to use in cases of apparent close host-parasite relationship in phylogeny as it may be derived from their recent relations.

– *Parasite complex of a given host in a given area.* In many cases two or more parasite species are often known to attack the same host in a given area. According to CHRISTMANN (1953), such a host is called a "mutual host" with respect to the parasite species, contrary to a "differentiated host", which is parasitized by a single parasite species in a given area.

– *Human activity.* Biological control research has shown certain parasites to be effective in the limitation of certain aphids. However, in many cases the hosts of these effective parasites established in nature were not found to be of economic significance, and research workers have tried to propagate other host aphids—the pests as new hosts in the laboratory and later in the field as well. The result—the original host aphids were classified as natural hosts, while the new hosts were mentioned as unnatural hosts.

When we have in mind the evolution of host-parasite relationship it is apparent that many aphids have also become unnatural hosts of parasite species through the spread via man's economy, etc. It would seem perhaps better to preserve the term "unnatural host" for the case of purposeful propagation of an aphid species as a new host of a given parasite. In case that laboratory host propagation is useful in the field as well, such a host becoming "natural" in this way, the origin of such a host has to be noted in the host list of the given parasite species in a similar way as the purposeful introduction of a parasite by man into a given area.

REFERENCES. 194, 696, 865-6, 984, 1118, 1125.

Parasite Classification

Parasitocoenosis is an association of organisms that inhabit a certain host (PAVLOVSKIY 1964). The aphid and parasite relationship is simple, representing one of its parts only, nevertheless, further members of aphid-parasite association such as hyper-parasites make the relations more complicated.

Various relations are known to occur, however, among various larvae.

– *Primary parasitism.* This is the relation between host aphid and a single parasite larva. Example: Aphidiid parasite larva of A-species present in a host aphid.

– *Superparasitism I.* In this case of relationship two or more primary parasite larvae of the same parasite species may be found in a single host aphid. Example: Two or more primary parasite larvae of an aphidiid A-species present in one host aphid.

– *Multiparasitism I.* In this case two or more larvae of two different species of primary parasites may be found in one host aphid. Example: two or more primary parasite larvae of aphidiid species A and B or another primary parasite species, present in one host aphid.

– *Hyperparasitism I or secondary parasitism.* In this case, a primary parasite larva and a secondary parasite larva are present in one host aphid. Example: Primary parasite larva of aphidiid A-species and a secondary parasite larva of A-species, the latter being either an external or internal parasite, present in one host aphid.

– *Hyperparasitism II or tertiary parasitism.* In such a case, primary parasite larva, secondary parasite larva and tertiary parasite larva may be found in the same host

aphid. The tertiary parasitism is caused by the relationship of internal and external hyperparasites, the latter being then in parasitic relationship to secondary parasite larvae. Example: Primary parasite larva of aphidiid A-species, secondary parasite larva of A-species and tertiary parasite larva of A-species present in one host aphid.

– *Hyperparasitism I – superparasitism II*. This is a case when two larvae of the same species of secondary parasites are present in the same larva of primary parasite in one host. Example: Primary parasite larva of aphidiid A-species, secondary parasite larva of A-species, and two or more tertiary parasite larvae of A-species present in one aphid.

– *Hyperparasitism I – multiparasitism II*. In this case, one primary parasite larva, one secondary parasite larva, and two or more tertiary parasite larvae of different species occur in a host. Example: Primary parasite larva of aphidiid A-species, one secondary parasite larva of A-species, and tertiary parasite larvae of A and B-species present in one host.

– *Hyperparasitism I – superparasitism II – multiparasitism III*. In this complicated case one primary parasite larva, two or more secondary parasite larvae of the same species, and tertiary parasite larvae of different species are present in one host. Example: Primary parasite larva of aphidiid A-species, secondary parasite larvae of A-species, and tertiary parasite larvae of A and B-species in one host aphid.

– *Hyperparasitism I – multiparasitism II – multiparasitism III*. Such a complicated case occurs if there are present a primary parasite larva, two or more larvae of secondary parasite larvae of different species, and two or more tertiary parasite larvae of different species in one host. Example: Primary parasite larva of aphidiid A-species, secondary parasite larvae of A and B-species, tertiary parasite larvae of A and B species.

– *Hyperparasitism I – multiparasitism II – superparasitism III*. Here primary parasite larva, two or more secondary parasite larvae of different species, and two or more larvae of the same tertiary parasite species are present in one host. Example: Primary parasite larva, secondary parasite larvae of A and B species, tertiary parasite larvae of A-species present in one host aphid.

– *Hyperparasitism I – superparasitism II – superparasitism III*. In this case, primary parasite larva, two or more secondary parasite larvae of the same species, and two or more tertiary parasite larvae of the same species are present in a host. Example: Primary parasite aphidiid larva of A-species, two or more secondary parasite larvae of A-species, and tertiary parasite larvae of A-species present in a host aphid.

Some of the possibilities mentioned above are of theoretical value; we know, however, of true examples up to the case of tertiary parasitism. Further possibilities are believed to be obtainable through laboratory experiments. Theoretically, even more combinations are possible, in multiparasitism and superparasitism.

– *PARASITES – PARASITOIDS*. DOULT (1959) has correctly mentioned that entomophagous Hymenoptera differ from the real parasites in many ways, so that the term "parasitoid" is proposed in order to distinguish both the groups. The main characters of parasitoids are as follows:

- (a) The development of an individual destroys its host.
- (b) The host is usually of the same taxonomic class, i.e. Insects.
- (c) In comparison with their hosts, they are of a relatively large size.
- (d) They are parasitic as larvae only, the adults being free-living forms.
- (e) They do not exhibit heteroecism.
- (f) As a parameter in population dynamics their action resembles that of predators more than of true parasites.

The aphidids fully fit in with this classification, representing therefore typical parasitoids. Nevertheless, in our opinion, equivalent terminology would be necessary

with respect to various kinds of parasitism, etc., in addition. For this reason, aphidiids are mentioned as "parasites" in our book, although the term "parasitoid" is believed to be well justified.

— SUBCATEGORIES OF PARASITISM. According to SWEETMANN (1958) various aspects may be applied when classifying different subcategories of parasitism.

(a) According to the kingdom to which the parasites belong, they may be either phytoparasites or zooparasites.

The aphidiids are typical zooparasites.

(b) According to the feeding site, parasites may be either ectoparasites (external parasites), or endoparasites (internal parasites). The aphidiids are endoparasites during their development, except for the adult stage.

(c) According to adaptation, parasites may be obligatory, facultative, or incidental. The aphidiids are obligatory parasites of aphids during their development except for the adult stage.

(d) According to succession of attacks, the parasites are either primary parasites or hyperparasites. The aphidiids are primary parasites exclusively.

(e) According to intensity of attack, simple parasitism and multiparasitism are distinguished. The aphidiids are typical simple parasites, multiple parasitism being found temporarily and resulting through competition, either inter- or intraspecific, again in simple parasitism.

(f) According to number of host species attacked. Usually, three types of parasitism are recognized: monophagous, oligophagous and polyphagous. Our studies on the host-specificity of aphidiids have shown that such a scheme is not suitable for the classification of the aphidiid wasps (STARÝ, 1964). The differentiation of the parasites into separate types instead of the above mentioned scheme has been used, being based on the relation of a parasite to a certain host species or host species group (for details see host specificity).

(g) According to number of hosts suitable for development, monoxenous and heteroxenous parasites are recognized. The aphidiids are typical monoxenous parasites.

(h) According to number of parasites on or inside the host, solitary and gregarious parasites are distinguished. The aphidiids are solitary parasites. Although gregarious parasitism is commonly found among the parasitic Hymenoptera, the apparently restricted space and food sources represented by a single host aphid, as well as the relative large size of an aphidiid, are apparently the main reasons why gregarious parasitism is not found among the aphidiids. Even in cases of the occurrence of two or more larvae inside a single aphid host due to super- and multiparasitism, competitive relations originate and only a single larva remains as a consequence, representing a practical proof of restricted environmental conditions by the host body size.

(i) According to the stability of infestation, permanent parasites and periodical or temporary parasites are distinguished. The aphidiids are typical periodical parasites, their adults exhibiting a free and non-parasitic mode of life.

(j) According to the tissues or organs attacked, parasites are distinguished into organotrophic or histotrophic groups (CHRISTMANN, 1953). The aphidiids may not be differentiated into such groups, getting both on organs and tissues of their hosts, although one type of feeding may be prevalent over the other one during the parasite larva development.

REFERENCES. 29, 184, 194, 211, 285, 290, 294, 419, 421, 456, 806, 866, 1118, 1125, 1163, 1303.

Aphid Groups and Their Parasites

Aphids as the hosts of parasites represent an important part of the environment as the parasites spend all their developmental period up to adult stage inside the bodies of their hosts. Consequently, relationship of different aphid groups and their parasites is a rather important subject in the research of parasite biology. We have mentioned the factors that influence these relations in the host specificity paragraph. The present one is to show those detailed relations between the separate groups of host and parasite as well as the relative values of taxonomy and ecology.

- TAXONOMIC GROUPS OF APHIDS. It is difficult to classify the exact relations of separate aphid groups and their parasites on the basis of world fauna as our knowledge is not equivalent in various parts of the distribution area of the family. For this reason, we have mostly used for this classification only such areas where we are more familiar with the fauna. In the classification of aphids the system used by СИЛАПОШНИКОВ (1964) has been followed.

- *Adelgoidea*. The whole of this group is not attacked by the aphidiid parasites. The biology of this group, which shows rather ancient features and numerous complications, has apparently been unsuitable to the parasites both in earlier and recent times. As we will show in the phylogeny chapter, the aphidiid parasites have adapted to parasitism on the aphids not earlier than when the Adelgoid and Aphidoid groups were separated. The parasites have adapted totally to the parasitism on the Aphidoid aphids. This adaptation has apparently the same features both in the past and present, as we are not aware of any secondary adaptation of parasites to parasitism on the Adelgoid aphids, although some of the biological features of this group are similar to those of the Aphidoid aphids (galls) and consequently a secondary adaptation could theoretically be found.

- Adelgidae, Phylloxeridae - The first family is associated with coniferous, the latter with deciduous trees. No aphidiid parasites are known.

- *Aphidoidea*

- Pemphigidae - This group, which is a very ancient one as to its origin, includes both holocyclic monoecious and dioecious species, anholocyclic is also known. They cause various galls on their main host plants, obligatory host alternation is connected with the attack of various herbs or even trees, where the aphids live mostly on roots, rarely on parts of plants above ground.

Apparently rather ancient and specialized genera may be found among some parasites that attack some of the gall aphids: *Monoctonia pistaciaecola* attacks *Pemphigus* and *Forda* species and exhibits rather close adaptation to the host life history (see: seasonal history). *Aroclon lepelleyi* attacks *Schizoneura* species and even *Eriosoma lanigerum*, the latter case being apparently a secondary adaptation of the parasite as the aphid has been introduced into Europe.

The gall aphids are also known to be attacked by widely specialized parasites (*Ephedrus plagiator*—*Asiphum*, *Schizoneura*, *Prociphilus*; *Ephedrus persicae*—*Thecabius*). On the secondary host plants, the root aphids are commonly attacked by widely specialized *Paralipsis enervis* (*Byrsocrypta*, *Forda*), the above ground aphids may be parasitized by widely specialized *Lysiphlebus fabarum* (*Pemphigus*).

- Lachnidae - This is an ancient aphid group which was associated previously with conifers, some groups have secondarily adapted themselves to deciduous woody plants.

All the parasites attacking the Lachnidae represent a strictly separated group from other aphidiid parasites.

The Cinarine aphids, which are associated with the conifers, are generally attacked

by various *Pauesia* species, which exhibit various degrees of specificity. *Metaphidius aterrimus* seems to show similar features. *Protolachnus* (Parasites—*Diaeretus leucopterus*, *Praon bicolor*) exhibit specialized parasites, the same as *Schizolachnus* (parasite: *Pauesia uilachni*).

The Lachnids associated with deciduous trees are parasitized by specialized parasites. *Stomaphis* (*Protaphidius* species), *Tuberculachnus* (*Aphidius salignae*), *Pterochloroides* (*Pauesia chlorata*), *Maculolachnus* (*Pauesia maculolachni*), *Lachnus* (*Lachnus tropicalis*—*Pauesia tropicalis*, *L. roboris*—no parasites).

No parasites are known to attack the Tramine group, which includes the anholocyclic species that occur on roots of various herbs and has a close association with ants. In our opinion, we can expect them to be attacked by *Paralipsis enervis*, which is a widely specialized parasite of various root aphids.

—Mindaridae—This ancient aphid group is known to be attacked by aphidiid parasites which attack Lachnidae, but the records must be verified.

—Anoeciidae—This ancient aphid group is associated with deciduous trees. Obligatory host alternation occurs and secondary host plants are various herbs (Gramineae).

Species of this group are attacked by widely specialized parasites: *Lipolexis gracilis* on primary host plants; *Paralipsis enervis* and *Aclitus obscuripennis* on roots of the secondary host plants. The range of the latter species is not sufficiently known, but it seems to be specialized in a similar way as the earlier mentioned species to parasitism on various root aphids.

—Phloemyzidae—No aphidiid parasites of this group are known.

—Thelaxidae—This is a typical forest aphid group, associated with deciduous woody plants. *Thelaxes* is attacked by the specialized *Lysiphlebus thelaxis*. *Glyphina* is parasitized by the less specialized *Aphidius sicarius*, which attacks other aphids associated with *Betula*.

—Greenideidae—This aphid group is restricted to subtropical and tropical areas of south-east Asia. The parasites attacking the Greenideid aphids are rather differentiated from parasites of other groups and manifest strictly specialized host range restricted to the Greenideidae. *Greenidea ficicola* is attacked by *Archiaphidius greenideae* and *Trioxys (Fissicaudus) confucius*.

—Hormaphididae—The shape of body, wax covers, etc., as extreme modifications in aphids resembling the coccids, resulted in this aphid group mostly not being parasitized by the aphidiids. *Cerataphis*, which is distributed in the tropical belt, exhibits too a coccidoid type of body, so that its species are not attacked by the aphidiids at all. Morpho-ecological resemblance of these aphids to coccids is also apparent from their parasitism by some chalcids that mainly attack the aleyrodids, coccids, etc. *Oregma*—this is a similar case, nevertheless, *Lipolexis oreginae* is known as a parasite of one of the species from tropical Asia, besides the chalcids.

—Callaphididae—This is a very ancient aphid group. No obligatory host alternation occurs, only facultative host alternation is known. The members of this group may be more or less kept as indicators of certain floristic zones. Their parasites are strictly habitat dependent and mostly restricted to this group exclusively, while the widely specialized parasites (*Ephedrus plagiator*, *Lysiphlebus ambiguus*) attack this group relatively rarely.

We can distinguish several groups of aphids and associated parasites as follow, two of them are satisfactorily known.

Deciduous forest group (western Eurasia): *Symydobius*, *Betacallis*, *Euceraphis*, *Phyllaphis*, *Tinocallis*, *Tuberculoides*, *Betulaphis*, *Calaphis*, *Callaphis*, *Pterocallis*, *Encalpterus*, *Chromaphis*, *Myzocallis*, *Drepanosiphum*, etc. Among the parasites of this group we can distinguish relatively widely specialized species, which attack a great

part of Callaphidids in forest habitats (*Praon flavinode*, *Trioxys pallidus*); somewhat less specialized is *Aphidius sicarius* (*Betulaphis*, *Calaphis*, etc.). Strictly specialized parasites represent the third group: *Trioxys phyllaphidis* (*Phyllaphis*), *Trioxys hortorum* (*Tinocallis*), *Trioxys betulae* (*Symydobius*), and parasites of *Drepanosiphum* (*Dyscritulus planiceps*, *Monoctonus pseudoplatani*, *Trioxys cirsii*).

Deciduous forest (Far East Asia) group is represented by *Bioxys japonicus*, *Trioxys luteolus* (*Shivaphis* sp.), *Praon glabrum* (*Euceraphis*), but so far is not satisfactorily known.

Steppe group (western Eurasia) is represented by the following aphid groups: *Therioaphis*, *Iziphyia*, *Thripsaphis*, *Saltusaphis*, *Bacillaphis*. Most of them are attacked by the strictly specialized *Trioxys* species, to a lesser degree by *Praon* species (*Therioaphis*). *Diaeretellus macrocarpus* is widely specific in the frame of the group (*Iziphyia*, *Bacillaphis*, *Thripsaphis*).

Tropical rain forest (Neotropical region) is almost unknown. We found a rather primitive Callaphidid aphid, *Neolizerius* sp., to be parasitized by *Pseudephedrus neotropicalis* in the tropical cloud forest zone in Cuba. The parasite seems to be strictly specialized.

- Chaitophoridae - This is also an ancient aphid group. No obligatory host alternation is developed, only facultative host alternation occurs. Parasites are strictly habitat dependent and associated with different groups of their hosts. The Chaitophorid aphids are, in general, poorly attacked by widely specialized parasites (*Ephedrus plagiator*—*Chaitophorus* sp., *Sipha flava*—*Lysiphlebus testaceipes*).

Forest aphid species include two groups: *Chaitophorus* are attacked by strictly specialized *Lysiphlebus salicaphis*, which seems to be distributed all over the area of *Chaitophorus* distribution, although it attacks different species in various parts of the area. *Periphyllus* aphids are attacked by the specialized *Aphidius setiger* (Europe), *A. areolatus* (Far East Asia) and *Trioxys falcatus* (Europe).

Steppe aphid species are represented by the Atheroidine group (*Laingia*, *Atheroides*, *Chaetosiphella*, *Sipha*, *Caricosipha*). *Lysiphlebus arvicola* seems to be relatively widely specialized in the frame of this group (*Atheroides*, *Sipha*).

- Aphididae - This is the youngest group as to the evolution of aphids, which has covered a number of different zones and habitats during its evolution, attacking a great number of various plants. Both obligatory and facultative host alternation occurs.

The Pterocommatinae subfamily, associated with certain deciduous trees, is attacked by the strictly specialized parasite *Aphidius cingulatus* (*Pterocomma* species).

Among the parasites that attack the subfamily Aphidinae we can distinguish all the types of host range known in the aphidids. Although we have tried to deal with the separate groups of the Aphidinae, it seems preferable to mention the main representatives of the parasites to show their host specificity range, which covers the aphid groups to a different degree because of host specificity determining factors. We have used only the European fauna to illustrate the relations (see STARÝ 1968). A similar review may be obtained on the basis of other faunas; however, separate parasite species may exhibit other features in their host specificity range in other areas (see: Geographic distribution).

Ephedrus cerasicola. - Macrosiphina: *Myzus cerasi*.

Praon necans. - Rhopalosiphina: *Rhopalosiphum nymphaeae*.

Praon rosaeicola. - Macrosiphina: *Macrosiphum rosae*.

Aphidius caraganae. - Macrosiphina: *Acyrtosiphon caraganae*.

Aphidius equiseticola. - Macrosiphina: *Sitobium equiseti*.

Aphidius hortensis. - Macrosiphina: *Loasomaphis berberidis*.

- Aphidius megourae*. — *Macrosiphina*: *Megoura viciae*.
Aphidius mirotarsi. — *Macrosiphina*: *Mirotarsus cyparissiae*.
Aphidius phalangomyzi. — *Macrosiphina*: *Phalangomyzus oblongus*.
Aphidius souchi. — *Macrosiphina*: *Hyperomyzus lactucae*.
Lysiphlebus hirticornis. — *Macrosiphina*: *Metopeurum fuscoviride*.
Lysiphlebus melandriicola. — *Anuraphidina*: *Brachycaudus lychnidis*.
Monoctonus nevosus. — *Macrosiphina*: *Impatiensium balsamines*.
Trioxys auctus. — *Rhopalosiphina*: *Rhopalosiphum oxyacanthae*.
Trioxys genistae. — *Aphidina*: *Aphis genistae*.
Trioxys glaber. — *Aphidina*: *Aphis galii-scabri*.
Trioxys humuli. — *Macrosiphina*: *Phorodon humuli*.
Trioxys inaeocerasus. — *Aphidina*: *Aphis podagrariae*.
Trioxys panonicus. — *Macrosiphina*: *Titanosiphon artemisiae*.
Trioxys parvatus. — *Macrosiphina*: *Hyadaphis* sp.
Trioxys spinosus. — *Liosomaphidina*: *Scutaphis dauci seselii*.
Praon pubescens. — *Macrosiphina*: *Nasonovia nigra*, *N. ribisnigri*.
Aphidius absinthii. — *Macrosiphina*: *Macrosiphoniella absinthii*, *M. artemisiae*, *M. kaufmanni*, *M. millefolii*, *M. pulvera*, *M. scijuncta*, *M. stageri*, *M. xeranthemi*.
Aphidius hieraciorum. — *Macrosiphina*: *Nasonovia nigra*, *N. pilosellae*, *N. ribisnigri*.
Aphidius nigrescens. — *Macrosiphina*: *Aulacorthum geranii*, *A. spp.*
Monoctonus angustivalvus. — *Macrosiphina*: *Nasonovia nigra*.
Monoctonus crepidis. — *Macrosiphina*: *Nasonovia nigra*, *N. pilosellae*, *N. ribisnigri*.
Trioxys aculephae. — *Aphidina*: *Aphis crataegae*, *A. crataegivora*, *A. cytisorum*, *A. euphorbiae*, *A. fabae*, *A. farinosa*, *A. idaei*, *A. mordwilckiana*, *A. nasturtii*, *A. ruborum*, *A. salviae*, *A. spiraeophaga*, *A. urticae*.
Trioxys leifer. — *Liosomaphidina*: *Cavariella acgopodii*, *C. archangelicae*.
Ephedrus campestris. — *Macrosiphina*: *Dactynotus aeneus*, *D. cichorii*, *D. humilae*, *D. jaceae*, *D. muralis*, *D. obscurus*, *D. picridis*, *D. souchi*, *Macrosiphoniella absinthii*, *M. millefolii*, *M. inborni*, *M. tanacetaria*.
Ephedrus minor. — *Liosomaphidina*: *Myzaphis rosarum*, *Passerina tetrarhoda*.
Praon absinthii. — *Macrosiphina*: *Macrosiphoniella absinthii*, *M. millefolii*, *M. tanacetaria*, *Plectrochophorus* sp., *Titanosiphon artemisiae*.
Praon dorsale. — *Macrosiphina*: *Acyrtosiphon pisum*, *Dactynotus campanulae*, *D. carthami*, *D. cichorii*, *D. jaceae*, *D. linariae*, *D. obscurus*, *D. souchi*, *Paczoskia major*, *Megoura viciae*.
Aphidius avenae. — *Macrosiphina*: *Sitobium avenae*, *Sitobium granarium*.
Aphidius ervi. — *Macrosiphina*: *Acyrtosiphon pisum*, *A. caraganae*, *A. spartii*, *A. superbum*, *Macrosiphium rosae*, *Microlophium evansi*.
Aphidius funebris. — *Macrosiphina*: *Dactynotus aeneus*, *D. achilleae*, *D. campanulae*, *D. cichorii*, *D. picridis*, *D. souchi*, *Paczoskia major*.
Aphidius louiceae. — *Macrosiphina*: *Amphorophora ampullata*, *Aulacorthum dryopteridis*, *Macrosiphium daphnoides*, *M. gei*, *M. ordoencensis*, *M. preautluidis*, *M. stellariae*.
Aphidius ribis. — *Macrosiphina*: *Cryptomyzus ribis*, *Myzella galeopsidis*.
Aphidius rosae. — *Macrosiphina*: *Macrosiphium rosae*, *M. funestum*.
Aphidius rubi. — *Macrosiphina*: *Macrosiphium funestum*, *Nectarosiphum rubi*.
Aphidius tanacetarius. — *Macrosiphina*: *Metopeurum fuscoviride*, *Microsiphium millefolii*.
Aphidius transcaspicus. — *Rhopalosiphina*: *Hyalopteris pruni*, *Longiunguis donacis*.
Lysaphidius arvensis. — *Liosomaphidina*: *Lysaphis erysimi*, *Pseudobrevicoryne erysimi*.
Diaretellus eplippium. — *Macrosiphina*: *Decorosiphon corynothrix*, *Rhopalosiphum poae*.
Diaretellus heinzii. — *Macrosiphina*: *Decorosiphon corynothrix*.
Monoctonus caricis. — *Macrosiphina*: *Metopolophium festucae*, *Sitobium equiseti*.
Trioxys brevicornis. — *Liosomaphidina*: *Cavariella* spp., *Hyadaphis bupleuiri*, *H. foeniculi*, *H. mellifera*, *Staegeriella necopinata*.
Trioxys centaureae. — *Macrosiphina*: *Dactynotus aeneus*, *M. campanulae*, *M. cichorii*, *D. jaceae*, *D. muralis*, *D. obscurus*, *Macrosiphoniella artemisiae*, *M. millefolii*, *M. tanacetaria*, *Microlophium evansi*.
Ephedrus nachei. — *Aphidina*: *Cryptosiphum artemisiae*, *Liosomaphidina*: *Haylurstia atriplicis*.

Praon abjectum. — Rhopalosiphina: *Rhopalosiphum padi*, Aphidina: *Aphis bupleuri*, *A. craccivora*, *A. fabae*, *A. farinosa*, *A. sambuci*, *A. spiraeophaga*, *A. viburni*.

Aphidius matricariae. — Aphidina: *Aphis* sp., Liosomaphidina: *Hayhurstia atriplicis*, *Hyadaphis hoffmanni*, Macrosiphina: *Galiobium langei*, *Liosiphon galiophagus*, *L. asperulophagus*, *Myzus ajugae*, *M. cerasi*, *M. ligustri*, *M. persicae*, *M. ornatus*, *Capitophorus hipophaeae*.

Aphidius pascuorum. — Rhopalosiphina: *Rhopalosiphum padi*, Schizaphis *scirpi*, Macrosiphina: *Metopolophium dirhodum*, *Sitobium avenae*.

Aphidius picipes. — Anuraphidina: *Brachycaudus cardui*, Macrosiphina: *Myzus auctus*, *M. persicae*.

Aphidius salicis. — Aphidina: *Aphis lambersi*, *A. farinosa*, Liosomaphidina: *Cavariella* spp., *Semaphys dauci*.

Monoctonus cerasi. — Rhopalosiphina: *Rhopalosiphum padi*, *R. oxyacanthae*, Anuraphidina: *Dysaphis crataegi*, Macrosiphina: *Myzus ligustri*.

Ephedrus persicae. — Rhopalosiphina: *Rhopalosiphum padi*, Aphidina: *Aphis fabae*, *A. idaei*, *A. pomi*, *Brachyunguis* sp., *Toxoptera aurantii*, Anuraphidina: *Dysaphis crataegi*, *D. devector*, *D. plantaginea*, *D. sorbi*, *Roepkea marchali*, *Allocolaphis quaestionis*, *Brachycaudus helichrysi*, *B. lychnidis*, Liosomaphidina: *Hayhurstia tataricae*, *Hyadaphis melifera*, Macrosiphina: *Myzus cerasi*, *M. ligustri*, *Phorodon humuli*, *Geoktopia pyrarica*, other groups: *Thecabius* sp.

Ephedrus plagiator. — Rhopalosiphina: *Rhopalosiphum padi*, *R. nymphaeae*, *R. oxyacanthae*, *Schizaphis scirpi*, *Hyalopterus pruni*, Aphidina: *Aphis bupleuri*, *A. craccivora*, *A. fabae*, *A. farinosa*, *A. idaei*, *A. nasturtii*, *A. spiraeophaga*, *A. urticae*, *A. viburni*, Anuraphidina: *Dysaphis devector*, *D. crataegi*, *D. sorbi*, *D. tataricae*, *Ceruraphis eriophori*, *Brachycaudus cardui*, *B. helichrysi*, Liosomaphidina: *Liosomaphis berberidis*, *Hyadaphis foeniculi*, Macrosiphina: *Acyrtosiphon caraganae*, *A. spartii*, *Aulacorthum chelidonii*, *Hyperomyzus lactucae*, *Myzus cerasi*, *Phorodon humuli*, *Macrosiphum prenantioides*, *M. rosae*, *M. weberi*, *Sitobium avenae*, *S. equiseti*, other groups: *Asiphon* sp., *Chalcophorus* sp., *Myzocallis* sp., *Prociplus* sp., *Schizoneura* sp., *Sipha* sp., *Anoecia* sp.

Praon volucre. — Rhopalosiphina: *Rhopalosiphum padi*, Aphidina: *Aphis craccivora*, *A. grossulariae*, *A. idaei*, *A. pomi*, Anuraphidina: *Dysaphis* sp., *Brachycaudus helichrysi*, *B. lychnidis*, Liosomaphidina: *Trilobaphis* sp., *Lipaphis fritzmülleri*, *Brevicoryne brassicae*, *Semaphys dauci*, *Hyadaphis* sp., Macrosiphina: *Liosiphon galiophagus*, *Myzus ligustri*, *M. persicae*, *M. cerasi*, *Rhopalomyzus alpigenae*, *Rhopalosiphoninus* sp., *Nectarosiphum rubi*, *Aulacorthum aegopodii*, *A. geranii*, *Acyrtosiphon caraganae*, *Hyperomyzus lactucae*, *Microlophium evansi*, *Macrosiphum euphorbiae*, *M. rosae*, *M. gel*, *M. funestum*, *M. oregonensis*, *M. prenantioides*, *M. stellariae*, *Macrosiphoniella* sp., *Dactynotus ochropus*, *D. jaccoe*, *Sitobium avenae*, *S. fragariae*.

Diactietella rapae. — Rhopalosiphina: *Schizaphis scirpi*, *S. longicaudata*, Aphidina: *Aphis* sp., Anuraphidina: *Brachycaudus helichrysi*, *B. rumexicolens*, Liosomaphidina: *Brevicoryne brassicae*, *Hayhurstia atriplicis*, *Lipaphis fritzmülleri*, Macrosiphina: *Myzus persicae*, *Dactynotus* sp., *Sitobium* sp., *Galiobium langei*.

Lysiphlebus ambiguus. — Aphidina: *Aphis fabae*, *A. farinosa*, *A. podagrariae*, *A. schneideri*, *A. urticae*, *A. solanella*, *A. nerii*, *A. ruborum*, *A. sarothamni*, *Toxoptera aurantii*, Anuraphidina: *Brachycaudus* sp., Liosomaphidina: *Hyadaphis* sp., other groups: *Chromaphis* sp.

Lysiphlebus fabarum. — Rhopalosiphina: *Rhopalosiphum nymphaeae*, Aphidina: *Aphis chloris*, *A. clematidis*, *A. craccivora*, *A. euphorbiae*, *A. neoreticulata*, *A. fabae*, *A. hederiae*, *A. myrtili*, *A. klinckschlii*, *A. lambersi*, *A. newtoni*, *A. plantaginis*, *A. podagrariae*, *A. polygouata*, *A. pomi*, *A. poterii*, *A. roepkei*, *A. ruborum*, *A. runcis*, *A. solviae*, *A. sarothamni*, *A. stachydis*, *A. taraxacicola*, *A. thomasi*, *A. umbrellae*, *A. urticae*, *A. vanderghoffi*, *A. verbasci*, *Protaphis carlinae*, Anuraphidina: *Brachycaudus cardui*, *B. rumexicolens*, *B. tragopogonis*, *Dysaphis* sp., Macrosiphina: *Hyperomyzus lactucae*, *Microsiphum nudum*, *Pezoskidea major*, *Sitobium avenae*, other groups: *Pemphigus* sp.

Paralipsis eucervis. — Aphidina: *Aphis roepkei*, Anuraphidina: *Brachycaudus ballotae*, *B. cardui*, *B. mordwilkoii*, *Dysaphis crataegi*, other groups: *Anoecia* sp., *Forda* sp., *Tetraneura* sp.

Trioxys angelicae. — Rhopalosiphina: *Rhopalosiphum padi*, Aphidina: *Aphis cognatella*,

A. craccivora, *A. fabae*, *A. craccae*, *A. cytisorum*, *A. hederæ*, *A. farinosa*, *A. pomi*, *A. salviae*, *A. solanella*, *A. ruborum*, *A. sambuci*, *A. spiraeophaga*, *A. viburni*, *Toxoptera aurantii*, *Anuraphidina*: *Brachycaudus helichrysi*, *Ceruraphis eriophori*, *Dysaphis devecta*.

Lipolexis gracilis. — *Aphidina*: *Aphis euphleuri*, *A. craccae*, *A. craccivora*, *A. euphorbiae*, *A. fabae*, *A. hederæ*, *A. intybi*, *A. newtoni*, *A. origani*, *A. plantaginis*, *A. polygonata*, *A. pomi*, *A. ruborum*, *A. salviae*, *A. sedi*, *A. taraxacicola*, *A. vallei*, *Toxoptera aurantii*, *Anuraphidina*: *Brachycaudus cardui*, *B. helichrysi*, *B. mordvilkoii*, *Macchiatiella* sp., *Macrosiphina*: *Myzus cerasi*, *M. persicae*, other groups: *Anoecia* sp.

— Unclear cases — There is no doubt that we have still a very restricted knowledge of the aphidid parasites, of their fauna, distribution and host specificity. The same is true of parasite species as enemies of separate aphid species. Consequently, we cannot mention generally an aphid group or species, in which parasites are unknown up to now, that is not parasitized by the aphidids at all. Nevertheless, our present knowledge agrees that certain aphids are not attacked by the parasites. The *Traminae* are believed to fall also in the host range of *Paralipsis enervis*, although no records on their parasites are known as yet. V.D. BOSCH & STERN (1962) mentioned several *Callaphidid* species to be free of parasites: *Boernerina depressa*, *Crypturaphis grassii*, *Callaphis juglandis*, *Ctenocallis* sp. We have no material of parasites reared from these aphids either; literary records include a parasite species to attack *Callaphis juglandis* in Soviet C. Asia. *Lachnus roboris* in Europe is also known to be free of parasites.

— MORPHO-ECOLOGICAL GROUPS OF APHIDS

— *Gall and leaf-curling aphids*. Galls may represent a temporary or perpetuum niche of an aphid species during the season.

Galls as a temporary niche are rather common in aphids. A number of dioecious aphid species cause galls on their primary host plants, then leave the galls and emigrate to their secondary host plants, returning in the late season to their primary host plants, where they overwinter. For example, *Forda* species and their relatives have *Pistacia* species as their primary host plants and various *Gramineae* (roots) as the secondary host plants; *Pemphigus* species occur on *Populus* and then on roots of various *Compositae*; *Prociphilus* species occur on *Fraxinus* and then on roots of *Abies*; *Schizoneura* species on *Ulmus* and then on roots of various plants; *Tetraneura* species on *Ulmus* and then on roots of various *Gramineae*; *Dysaphis* species on *Malus* and on roots of various plants, etc.

On the other hand, galls can represent a perpetual niche for the whole season. Such aphids are *Eriosoma lanigerum*, *Cryptosiphum* species, *Hayhurstia atriplicis*, and others

Simple galls are rather common in aphids. This type of galls includes leaf curling as well as various slight deformities due to aphid sucking. *Aphis idaei* on *Rubus*, *Myzus cerasi* on *Prunus avium*, *Brachycaudus helichrysi* on *Prunus persica*, *Myzus persicae* on certain plants, *Cryptosiphum artemisiae* on *Artemisia*, etc., may be mentioned as examples of leaf-curling aphids (Fig. 248). *Cryptomyzus ribis* causes a thickening of leaves in areas which are attacked by the aphids (Fig. 247).

Shoot axis galls, *Eriosoma lanigerum*. The sucking of aphids causes a bulging out of the cortex, irregular fissures appearing as a results (Fig. 258). *Pemphigus lichtensteini* causes development of massive galls on axis of *Populus*.

Bud galls occur in rudiments of leaves, branches, etc. Examples: Adelgoid aphids.

Leaf galls. Petiole galls: *Pemphigus spirothecae* causes subglobose to pyriform, spirally twisted galls on petioles of *Populus* leaves (Fig. 249). Fold galls: These galls arise due to unfolding of leaves. Example: *Forda* sp. (Fig. 250). Roll galls: They arise due to upward or downward rolling of a leaf, the gall being a tubular one. Example: *Hayhurstia atriplicis*. Pouch galls: They are the dominant type of leaf



Fig. 247. *Cryptomyzus ribis* on *Ribes rubrum*. Leaf-curling.

Fig. 248. *Cryptosiphum artemisiae* on *Artemisia* sp.

Fig. 249. *Pumphius* sp. galls on leaves of *Populus* sp.

Fig. 250. Galls caused by *Forda* sp. on *Pistacia lentiscus* leaves.

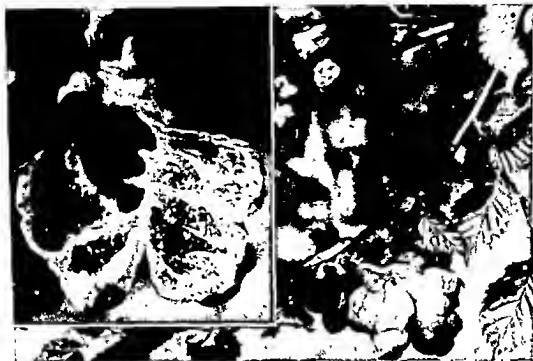


Fig. 251. *Schizoneura lanuginosa* galls on *Ulmus* sp. Left: - dissected gall, right: closed galls.

galls. They may be of various sizes and shapes, originating as a greater or smaller deformity of a leaf. Examples: *Schizoneura lanuginosa* on *Ulmus*, *Pachypappa vesicalis* on *Populus alba*, *Byrsocrypta ulmi* on *Ulmus* (Fig. 251).

A gall is usually produced by the fundatrix action. There may be, however, even another procedure in some pocket leaf galls. The fundatrices of *Forda* spp. form a temporary gall, which is small and always remains open. The fundatrix produces the progeny, but the latter leaves the gall and settles on the adjacent young leaflets and produces the characteristic leaf gall (BODENHEIMER & SWIRSKI, 1957).

The appearance of galls is closely dependent on climatic conditions, that determine the plant growth and aphid appearance. As they represent a result of plant response to aphid sucking, the galls appear in a certain stage of plant growth; they appear mostly at the most intensive stage of plant growth.

After a certain number of generations have developed, the gall opens and thus enables the aphids that occur inside it to get out. The period of gall opening is apparently dependent on the senescence of corresponding plant tissues.

Several generations of aphids can develop inside a gall. BODENHEIMER & SWIRSKI (1957) mention 2-3 generations in galls in *Fordinae* aphids in Israel.

It is obvious that a parasite ♀ is not capable of invading a closed gall. Simple galls and curled leaves can obviously be visited at any time and a rather strict coincidence does not seem to be necessary in parasites of such aphids (*Ephedrus plagiator*, *E. persicae*, etc.). However, a strict coincidence does apparently occur in closed galls, as the parasite ♀ must attack the aphids either before the gall is closed, or after it opens. Consequently, we may observe an apparent coincidence in the occurrence of fundatrices of *Forda* and *Pemphigus* species, and their parasite, *Monoctonia pistaciicola*. On the other hand, *Arcopraon lepelleyi* seems to be limited as to its occurrence to the period when galls of its host, *Schizoneura lanuginosa* open and the parasite ♀ can invade the gall through the holes and attack the aphids inside the gall.

Gall community is a highly specialized and complex community. A primary gall community is associated with the gall during its active phase of development and growth, before the escape of the aphids. A secondary gall community inhabits the gall after the escape of aphids (MANI 1964).

The relations inside a gall are rather complicated. There may be also other aphids, not participating in causing the gall in a given plant, but which found the gall to be a suitable niche. Parasites that are associated with such secondary gall inhabiting aphids may or may not infest both the aphid species in a gall. For example, we have found *Pachypappa vesicalis* to cause galls on *Populus*, in which there were also *Chaitophorus* species as secondary inhabitants. Similarly, mixed colonies of aphids exist in *Dysaphis* spp., where either two *Dysaphis* spp. are mixed, or *Dysaphis* species is mixed with *Aphis pomi*, etc.

Parasites are mostly inhabitants of primary gall communities as their adults lay eggs in living aphids that occur inside the galls. The period of oviposition is dependent on the type of gall and parasite species. However, some parasite species enter quiescent states and their quiescent cocoons can then be found in empty galls, the parasites are consequently—although being in a quiescent state—also members of secondary gall communities (*Ephedrus persicae*, *Monoctonia pistaciaecola*). In the case that there are also some aphids as occasional secondary inhabitants of galls (see above), the parasites may or may not attack both the species. In the above case of *Pachypappa* and *Chaitophorus* species, *Lysiphlebus salicaphis* attacked only the second aphid. In *Dysaphis* species and *Aphis pomi*, the parasites can attack both aphid species (see: EVENHUIS 1966).

Galls are not caused by a single species or aphid group. Many aphid groups participate in causing the galls. Consequently, a number of parasites can be recognized that attack the gall aphids. Among these parasites, we distinguish various degrees of specificity range with respect to the kind of gall and taxonomic relations of its host.

Lysiphlebus desertorum. It seems to be a specialized parasite of *Cryptosiphum* spp. in Asia (simple gall and leaf curling).

Aphidius ribis is restricted to *Cryptomyzus ribis* (simple gall).

Ephedrus cerasicola seems to be restricted to *Myzus cerasi* (simple gall-leaf curling).

Diaretetiella rapae attacks *Hayhurstia atriplicis* (roll gall) but it attacks also a number of freely living aphids.

Ephedrus nacheri attacks *Cryptosiphum* species (simple gall-leaf curling) and *Hayhurstia atriplicis* (roll galls). The parasite seems to be adapted to the niche, both the groups are not related taxonomically.

Monoctonia pistaciaecola attacks *Forda* species (leaf-fold gall) and *Pemphigus* species (petiole galls). It seems to be restricted to the Pemphigine aphids (gall producing species).

Acreopraon lepelleyi attacks *Schizoneura ulmi* (pouch galls), and even *Eriosoma lanigerum* (shoot axis galls). It seems to be restricted to galls of the Pemphiginae.

Ephedrus persicae attacks *Rhopalosiphum padi* (simple galls—leaf curling), *Aphis fabae* (simple gall-leaf curling), *Aphis idaei* (simple gall—leaf curling), *Aphis pomi* (simple gall—leaf curling), *Hyalopteris pruni* (simple gall—leaf curling), *Alloctaphis quae-stionis* (simple gall—leaf curling), *Dysaphis* spp. (simple gall—leaf curling), *Brachycaudus helichrysi* (simple gall—leaf curling), *Hyadaphis mellifera* (simple gall—leaf curling), *Myzus ligusuri* (roll gall), *Myzus cerasi* (simple gall—leaf curling), *Geok-tapia pyrararia* (roll gall), *Hayhurstia tataricae* (simple gall—leaf curling), *Phorodon humuli* (simple gall—leaf curling), etc. It attacks also some freely living species.

Ephedrus plagiator: *Rhopalosiphum padi* (simple gall—leaf curling), *Aphis fabae* (simple gall—leaf curling), *Aphis nasturtii* (simple gall—leaf curling), *Aphis idaei* (simple gall—leaf curling), *Hyalopteris pruni* (simple gall—leaf curling), *Aphis pomi*

(simple gall—leaf curling), *Ceruraphis eriophori* (simple gall—leaf curling), *Dysaphis* sp. (simple gall—leaf curling), *Brachycaudus cardui* (simple gall—leaf curling), *Myzus cerasi* (simple gall—leaf curling), *Hyperomyzus lactucae* (simple gall—leaf curling), *Schizoneura ulmi* (pouch gall), *Prociphilus fraxini* (simple gall—leaf curling), etc. It attacks a number of freely living aphids as well.

The following parasites sometimes infest gall aphids, but they are mostly attached to other aphid groups:

Lysiphlebus ambiguus: *Aphis schneideri* (simple gall—leaf curling).

Lysiphlebus fabarum: *Aphis fabae* (simple gall—leaf curling).

Praon abjectum: *Aphis fabae* (simple gall—leaf curling).

Trioxys angelicae: *Aphis pomi* (simple gall—leaf curling), *Dysaphis* sp. (simple gall—leaf curling), *Aphis fabae* (simple gall—leaf curling).

Lipolexis gracilis: *Myzus cerasi* (simple gall—leaf curling), *Aphis fabae* (simple gall—leaf curling), *Brachycaudus helichrysi* (simple gall—leaf curling).

The galls of Adelgids generally are not attacked by any of the aphidiid parasites. The life-history of these aphids and lack of parasite adaptation are the main reasons. — *Aphids occurring in crevices of bark*. *Stomaphis* species attack various deciduous trees. They can often be found in deep crevices of bark, where the bark is not so thick and the aphids can reach the inner plant tissues by their rostrum.

Parasites of *Stomaphis* species, i.e. *Protaphidius* species are apparently well adapted morpho-ecologically. The apical portion of the ♀ abdomen of these parasites is tubularly narrowed and telescopic, and rather long when the parasite oviposits. This adaptation enables the parasites to reach their hosts even in deep crevices where the usual manner of attack as used generally by the aphidiids would be hardly successful.

We have also observed *Panesia grossa* parasite to oviposit in *Todolachnus abieticola*. These aphids sometimes occur in bark crevices of trees as well, where the parasite ♀ is able to reach them by an extremely projected abdomen when ovipositing.

— *Aphids occurring in leaf sheaths*. Leaf sheaths as a microhabitat are found in various aphids. Some of them are as follows:

Rhopalosiphum maidis is a pan-tropical and subtropical species. Leaf sheaths of its host plants, the Gramineae, are the prevalent niche, but when the population is more numerous the aphids may occur freely in the neighbourhood of leaf-sheaths as well. This aphid biology is very typical and can be observed everywhere in the tropical part of its distribution area, but it seems to enable the occurrence of the aphid in an arid zone too. BODENHELMER & SWIRSKI (1957) observed that in Israel the aphid inside the rolled blade is well sheltered from the wind and the humidity is so high that vapour condensation takes place; this, together with the exudation of the plant, often results in the accumulation of a considerable amount of water inside the rolled blade, which provides the aphid during the summer with an actually tropical microclimate. (Fig. 264).

Some *Dysaphis* species can be mentioned as examples of this ecological group as well. They occur in leaf sheaths of their secondary host plants, both if being holocyclic or anholocyclic (tropics) (Fig. 252).

The research of parasites of these aphids has shown that they are attacked by parasites which attack freely living aphids apparently, this type of niche is not distinguished by *Lysiphlebus testaceipes*.

— *Root aphids*. Root aphids seem to be distinctly divided into two groups:

A.) The first group includes the underground and above ground aphids, whose occurrence on roots or root collars is temporary and they disperse gradually to other parts of plants. To such aphids belong for example *Aphis lambersi*, *A. plantaginis*, *A. poterii*, *A. taraxacicola*, *A. thomasi*, *A. vanderghooti*, *A. scaliai*, *Brachycaudus tragopogonis*,

Gall community is a highly specialized and complex community. A primary gall community is associated with the gall during its active phase of development and growth, before the escape of the aphids. A secondary gall community inhabits the gall after the escape of aphids (MANI 1964).

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(simple gall—leaf curling), *Ceruraphis eriophori* (simple gall—leaf curling), *Dysaphis* sp. (simple gall—leaf curling), *Brachycaudus cardui* (simple gall—leaf curling), *Myzus cerasi* (simple gall—leaf curling), *Hyperomyzus lactucae* (simple gall—leaf curling), *Schizoneura ulmi* (pouch gall), *Protaphidius fraxini* (simple gall—leaf curling), etc. It attacks a number of freely living aphids as well.

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Lipolexis gracilis: *Myzus cerasi* (simple gall—leaf curling), *Aphis fabae* (simple gall—leaf curling), *Brachycaudus helidrysi* (simple gall—leaf curling).

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— *Root aphids*. Root aphids seem to be distinctly divided into two groups:

A.) The first group includes the underground and above ground aphids, whose occurrence on roots or root collars is temporary and they disperse gradually to other parts of plants. To such aphids belong for example *Aphis lambersi*, *A. plantaginis*, *A. poterii*, *A. taraxacicola*, *A. thomasi*, *A. vanderghooti*, *A. scallai*, *Brachycaudus tragopogonis*,



Fig. 252. *Dysaphis apifolii* in leaf-sheath of *Phoeniculus vulgare*.

Fig. 253. Mummified *Brachycaudus mordwilkoii* on roots of *Echium vulgare*.

B. mordwilkoii, *Cinara kochiana* (PONTIN 1960), *Dysaphis crataegi*, *D. subterranea*, *Protaphis carlinae*, *Pemphigus* aphids, *Tetraneura ulmi*.

We can divide the parasites of aphids belonging to this group into two parts: In the first group belong parasites generally adapted to parasitism on aphids living on parts of plants above ground, but they may attack their hosts even when they occur on roots, root-collar, etc.; apparently, various holes in ant-nests (see: ant-attendance and parasites) may play a part in enabling the parasites to search for their hosts even in the inside of ant runs. Such parasites are e.g. *Lysiphlebus fabarum*, *Lipolexis gracilis*, etc. These parasites are neither morphologically nor ecologically adapted to life in underground habitats or to ant-attendance. The second group includes parasites that attack only true root aphids or root collar aphids, but they never attack these aphids when living on parts of plants above ground. *Paralipsis enervis* is a representative of this group; it is adapted both morphologically (heavily built) and ecologically (relations to ants). This parasite seems to be a widely specialized species, attacking various root aphids irrespective of their taxonomic relations, as the data on its host specificity range show: *Anecia* sp., *Aphis roepkei*, *Brachycaudus ballotae*, *B. cardui*, *B. mordwilkoii*, *B. spp.*, *Dysaphis crataegi*, *D. subterranea*, *Forda fornicaria*, *Forda marginata*, *Tetraneura ulmi*. (Fig. 253).

B.) The second group of root aphids includes such aphids that are restricted to underground life exclusively, either as a group (Tetraneurae) due to general anholocycly, or such aphid groups as some *Forda* species which manifest exclusively an underground mode of life in a part of their distribution area where they are anholocyclic (N. and C. Europe), but they are holocyclic in other parts of their distribution area.

As to the parasites attacking these aphids of the second group, *Forda* species are attacked by *Paralipsis enervis*, which is a common parasite of various root aphids (see: above). However, up to the present time, we do not know any parasites of the Tetraneurae.

= *Aphids occurring as free colonies*. This is the most numerous group among the aphids. Some aphid species may live as free colonies during the whole season. There are, for



Fig. 254. *Aphis hederæ* on *Hedera helix*.

example, *Aphis fabae*, *A. sambuci*, *Acyrthosiphon pisum*, *Macrosiphoniella* and *Dactynotus* species, and others. Another group of aphids may show such a type of life only during a certain part of the season. For example, *Rhopalosiphum padi* which is a leaf curling species on *Prunus padus* in spring, lives in free colonies on its secondary host plants, the Gramineae, during summer. Many aphid species occur in spring as root collar aphids, often being sheltered also in ant-runs, and later in the season they may be found to live freely on the parts of their host plants above ground. Host plant response to aphid attack may also have an influence: *Myzus persicae* causes heavy leaf-curling and deformation in *Cucumis sativus*, while it causes almost no deformation in *Solanum tuberosum*.

Parasites of aphids that live in free colonies represent a numerous group. Their host range is various. Some of them appear to be adapted more to this free colonial type of aphid occurrence, the others are restricted to a given aphid group (see host specificity). Microclimatic differences in the occurrence of separate free colonies can also be responsible for the differences in parasite preference (see, e.g. MCLEOD, 1937, etc.).

— *General morpho-ecological adaptations.* The microhabitat of aphids deeply influences their morphological features. NEVSKY (1929) recognized several aphid groups in this respect. They are believed to be significant with respect also to the parasites.

Aphids—xerobionts live on xerophytic plants in deserts, or mesophytic ones but

growing in open stands, that are not protected from the influence of sunshine. The occurrence of aphids on such plants is characterized by great insolation and temperature, dryness of air, intensity of evaporation and open exposition under poorly developed leaves. The adaptation of aphids is through maximal reduction of the evaporation surface (*Xerophilaphis*, *Xerobion*, *Brevicoryella*, *Cryptosiphum*, etc.): they are generally small in size, the siphuncles and cauda are abbreviated, the cuticle is areolated and wax cover is common. Some of them occur inside pseudogalls as well (*Cryptosiphum*).

At the present time, we know only a single parasite, *Lysiphlebus desertorum*, which has been described as a parasite of a typical xerobiont aphid, *Cryptosiphum* sp., from C. Asia. The other parasite of *Cryptosiphum* species, *Ephedrus nacheri*, attacks also another aphid, *Hayhurstia atriplicis* and it seems to be adapted to certain groups of gall aphids.

Aphids that live freely on leaves of trees and herbs, especially on the upper side, are oval and flat; this enables them to stay fixed on the surface and survive rain etc. They often have heavy wax covers, move little and are poorly pigmented.

Aphids occurring inside curled leaves, in semi-sheltered stands, exhibit an oval convex shape.

Aphids occurring on trunks and branches are usually large in size, with well developed siphuncles, cauda and antennae. They are poorly adapted to unfavourable external influences (rain) but their legs and wings are well developed and they are rather mobile, they often fall to the ground if disturbed, etc.

Aphids occurring in restricted spaces (galls) or terricolous aphids are almost globular in shape, with a wax cover and their legs and antennae are minute.

— *Solitary and gregarious aphids.* Aphid species that exhibit a solitary occurrence of individuals, are comparatively rare among the aphids (*Hornuaphidula*). We know nothing about their parasites.

Most aphids occur both in a solitary or gregarious manner in nature. BODENHEIMER & SWIRSKI (1957) ascertained that there are apparent differences among the separate species, the gregarious behaviour being of several types: In the apterous adults and nymphs, in a number of aphids, such as *Brevicoryne brassicae*, *Hyalopterus pruni*, *Pterochloroides persicae* and many others the young nymphs do not leave the mother for any distance, as long as the host conditions are favourable. Dense aggregations of nymphs of a first and even second generation can be found around the mother. We have observed even a third generation in *Hyalopterus pruni* whose colonies originated by a single fundatrix cover the whole of a mature *Prunus* leaf. Conditions of the host plant may affect and obscure this type of behaviour in a rather significant way. For example, *H. pruni* can cover the whole surface of host plant leaf, both in *Prunus* and *Phragmites* hosts; as the leaf becomes senescent, the aphids disperse over the surface of the same or even other leaves, exhibiting an almost "solitary" behaviour; this is namely in aphids on *Phragmites communis* during the summer.

In *Myzus persicae* there is a different behaviour in young nymphs. They do not prolong their stay around their mother aphid, but they disperse quickly all over the leaf. *Pyrolachnus* species show a similar behaviour, as not even the smallest aggregation was observed (BODENHEIMER & SWIRSKI, 1957).

Later behaviour seems to be possibly also obscured by the influence of host plant species. In *Myzus persicae* we have observed the typical dispersive behaviour on *Brassica* leaves in a greenhouse, but not on *Asparagus* or *Bougainvillea* plants, where there were dense aggregations of both aphid adults and nymphs around the stems and at the tops of the plants. In *Pyrolachnus* species, which are attached to coniferous trees, this influence of host plant is obvious.

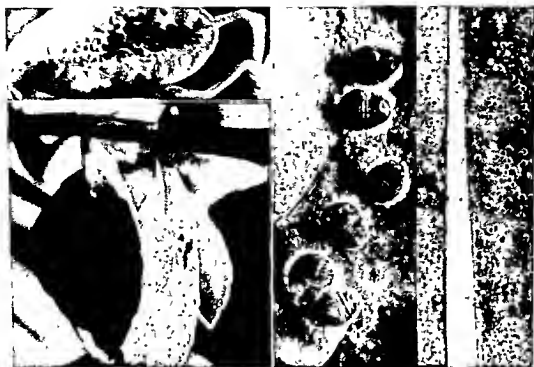


Fig. 255. *Toxoptera aurantii* on leaves of *Citrus* sp.

Fig. 256. *Cerataphis variabilis* on leaves of *Cocos nucifera*.

In alate adult aphids, both obligatorily (vagrants) and facultatively (migrants) host alternating species, there is usually no tendency to originate such aggregations. *Drepanosiphum platanoideis* seems to be an exception, it spends the summer diapause in alate adult stage, in typical aggregations, as observed by KENNEDY (1966).

Aggregations of aphids can markedly influence the preference and even attack of separate colonies by the parasites. For example, GEORGE (1957) observed that in *Brevicoryne brassicae* the percentage of parasitism by *Diacretella rapae* was the highest on the upper leaves, where the colonies of aphids were small and diffuse, while on the middle and lower leaves, where the aphid colonies were more dense, the parasite tended to restrict oviposition to the individuals at the edges of the colony.

Some parasite species are obviously able to find a host colony, while solitary aphids remain free; this seems to be the case of *Lysiphlebus fabarum*. On the other hand, *Aphidius ervi* is an example of a parasite species which exhibits a high searching ability as it is able to find even the rather dispersed and solitary fundatrices of its host in spring, not to mention smaller or larger colonies.

— *Ant-attended aphids*. The degree of ant-attendance in various aphid species resulted in a corresponding adaptation. We have dealt with this question separately.

— *Aphids producing audible sounds*. *Toxoptera aurantii* (Fig. 255) is reported by GRIFFITHS & THOMSON (1957) to behave as follows: as with most aphids, it may be noted, that periodically the entire colony seems to stand on their heads. It was observed that when the aphids stood on their heads they emitted a rasping scratching sound. *T. aurantii* is not attacked by a specialized parasite or a complex, consequently, we can say that this peculiar behaviour has no significance with respect to the parasites.

— *Coccidoid shape of aphid body*. In certain aphid groups the body shape is oval and subarcuate enabling them to exist safely on the exposed parts of plants. *Cerataphis* species, however, seem to be a little extreme, they resemble more coccids than they do the aphids as to their shape and occurrence on leaves. We do not know

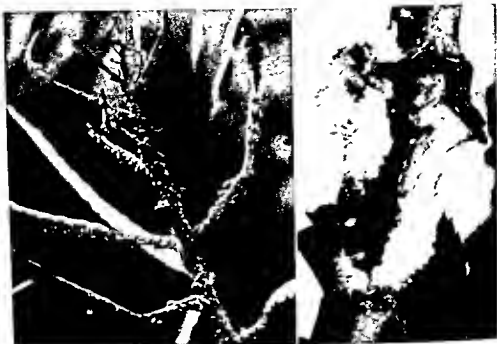


Fig. 257. *Brevicoryne brassicae* on *Brassica napus*.
Fig. 258. *Eriosoma lanigerum* on *Malus silvestris*.

any aphidid parasites attacking the *Cerataphis* species. Apparently, this shape of aphid body has become very different from that which we designate to be "aphidoid", to which the aphidids are adapted. The coccidoid resemblance seems to be stressed by the fact that *Cerataphis* species are attacked by *Encarsia* chalcids and these parasites are just typical parasites of coccids, aleyrodids, etc.; it seems that the morpho-ecological resemblance of the *Cerataphis* species to coccids is the main reason (Fig. 256). *Thelaxes* species exhibit similar morpho-ecological characters, nevertheless, these features do not reach an extreme degree as in *Cerataphis* species. Consequently, *Thelaxes* species are attacked by a specialized aphidid parasite, *Lysiphlebus thelaxi*.

— *Waxy coverings on aphid body.* Heavy wax production may be recognized in aphids of different groups and ecology. We see it in gall aphids and leaf-curling aphids living in forest type habitats (*Schizoneura ulmi*, *Stagona xylostei*, *Hyadaphis mellifera*, *Prociphilus* species, *Eriosoma lanigerum*) as well as in many species that live in desert habitats.

Wax cover produced by aphids may often cover the whole colony, so that no aphids are visible under it. This is the case of *Eriosoma lanigerum* (Fig. 258), *Hyadaphis mellifera*, etc. The aphidids are able to attack such aphids, although they do not seem to belong to their preferred hosts: *H. mellifera* is rarely attacked by *Ephedrus persicae* in Europe, the parasite is specialized mostly to parasitism on gall and leaf curling aphids; consequently, the wax cover seems to be less important than the mode of aphid life. *Eriosoma lanigerum* in Europe was reported to be attacked by *Areopraon lepeleyi* in England; the parasite adaptation is apparently of a secondary character, as it is known to attack gall aphids such as *Schizoneura* species in Europe.

In other species of aphids the wax cover may be rather strong, but we can separate the individual aphids. *Brevicoryne brassicae* is a typical representative (Fig. 257). It is attacked by several parasites, which seem to be well adapted. *Diaeretiella rapae*, the



Fig. 259. *Tuberculatus salignus* on *Salix* sp.

most common species, is, however, mentioned to restrict its attacks to these individuals of the aphid which are at edges of the colony.

GRIFFITHS (1960) made experiments with the influence of the wax cover of *Macrosiphum euphorbiae*, which has a slight wax cover, and of *Brevicoryne brassicae*, both the aphids being propagated as unnatural hosts of *Monoctonus crepidis*, which is a specialized parasite of *Nasonovia* species. This parasite tried intensively to clean itself after coming into contact with *M. euphorbiae*, and it generally avoided *Br. brassicae*. When contaminated there were even signs of fatal damage due to wax covers. GRIFFITHS (1961) believed this to be due to the behaviour of the parasite, which places its fore legs on the attacked aphid, a feature that does not occur in *D. rapae*. Nevertheless, in our opinion, this is caused by poor general adaptation of the parasite, but not by the type of oviposition behaviour as we know *Praon* species to attack *Br. brassicae* quite successfully placing its fore legs on the attacked aphid in a manner which is typical for the whole genus *Praon*.

The role of wax cover in *Br. brassicae* may be influenced by R.H. The wax cover is developed to a lesser degree in higher R.H. conditions, such as those in greenhouses.

Another example of wax cover in aphids represents *Tuberculatus salignus*, where the wax forms two remarkable thorns on the dorsal abdominal portion of the aphid (Fig. 259). Nevertheless, this aphid is attacked by a specialized parasite, *Aphidius salignae*, in Far East Asia.

The degree of wax covers may play a different role in host preference by parasites. For example, *Diaretella rapae* apparently prefers wax producers such as *Brevicoryne brassicae* or *Hayhurstia atriplicis*, but attacks less commonly *Myzus persicae*, where the wax cover is poor. On the contrary, according to SCHEURER (1964), *Lachnietta costata* was found to be parasitized by *Pauesia* species to a lesser degree apparently because of its highly developed wax cover, which is uncommon in other *Cinara* species.

— *Modifications of legs.* Saltatorial legs are developed in some Callaphidid aphids such as *Drepanosiphum*, *Tinocallis*, *Callipterus*, *Saltusaphis*, *Phyllaphis*, *Iziphyta*, *Therioaphis*, etc. Some aphids of these groups are able to jump in all stages (*Therioaphis*, *Drepanosi-*

phum, etc.); in others the ability to jump is restricted only to the adult stage: *Callipterus*, for example, is able to jump in the alate adult stage only. Saltatorial legs were believed to be a peculiar feature of aphids that require a corresponding adaptation in parasites: thus SCHILINGER & HALL (1960) believed that the oviposition behaviour in *Praon exoletum* reveals such an adaptation in placing its fore legs on the attacked aphid to overcome the jumping habit of the aphid; nevertheless, in our opinion, this ovipositional habit is typical of all species of the genus *Praon* and probably of *Monoclonus* as well; as the other species of the mentioned genera attack non-jumping aphids too, it is apparent that it is a common oviposition behaviour of these groups, not an adaptation to the host behaviour. SCHILINGER & HALL (1961) also believed that accessory prongs in *Trioxys complanatus* have a similar role in preventing the aphid from jumping and escaping. Nevertheless, also in this case, holding the attacked aphid between the prongs and ovipositor sheaths is a general oviposition behaviour of all the *Trioxys* species and it has a primary role in preventing an attacked aphid from escaping, irrespective of whether it is a jumping or non-jumping species. As there are also other parasites (*Aphidius*) that attack the jumping aphids, which do not have any apparent morpho-ecological adaptation in oviposition behaviour, it is apparent that the jumping of aphids depends on closely specialized oviposition behaviour of a parasite (length of oviposition act, antennal tapping, etc.). The above mentioned parasite adaptations are not more significant than in other groups, although parasites of the Callaphidid aphids are mostly strictly specialized to parasitism on this aphid group.

Prolonged tarsal segments are a character known to occur in the Traminae subfamily of the Lachnidae. It is probably the result of a close adaptation of these aphids to ant-attendance. As we do not know any parasites of this group, the significance of this adaptation with respect to parasites remains to be classified.

— *Length of rostrum.* The length of the rostrum is a convergent character which has a definite functional value in aphids. Accordingly, a long rostrum can be found in aphids that live on hairy plants. For example, *Corylobium* species living on the hairy plants of *Corylus* and *Acyrtosiphon* species have a long rostrum when living on long-haired hosts, while the rostrum is short on short-haired hosts (BODENHEIMER & SWIRSKI 1957). A long rostrum is also typical of the aphid species attacking plants having rather thick bark (*Stonaphis* species).

The length of the rostrum of aphids does not seem to have any significance with respect to their parasites. In some cases, the degree of hairiness of a plant could have a certain role, perhaps more important than the host aphid adaptation. The length of the rostrum might also be important in defense or escape reactions of attacked aphids, as the long rostrum means that the aphid escapes more slowly due to its attachment to the plant than if it had a short one; these aphids can easily pull their rostrum out of the plant and run off or fall down. However, the aphid responses seem to be specific.

— *Absence of siphunculi and wax glands.* This is a feature of typically ant-attended aphids. It does not seem to have any particular significance with respect to parasites. *Paralipsis eneris*, a typical parasite of many root aphids, attacks both more or less specialized ant-attended aphids.

— *Small dorsal tubercles.* This is mentioned to be typical of aphids associated with the Rosaceae (BODENHEIMER & SWIRSKI 1957). Aphids of this type are attacked by a number of parasite species. However, the morphological features mentioned do not seem to have significance in this respect.

— *Unclear cases.* As we have already mentioned in the foregoing taxonomic groups of aphids and parasite relationship, there are certain aphid groups or species which are not attacked by aphidid parasites. Some ecological peculiarities have not been recognized in the Aplanoid aphids.

— BIOLOGICAL CONTROL. In the aforementioned, we have tried to show the main features of the aphid taxonomical and ecological groups with respect to parasites. This general knowledge or at least its principles are rather important in a biological control program, which we start with the general classification of a given pest species. When we have a general knowledge of its taxonomic relations, life history, and distribution, we can theoretically predict certain relations of parasites to this aphid. For example, if we have to control an Adelgoid aphid it is obvious that aphidiids are of no use as they do not attack this aphid group at all. Or in the Calaphidid aphids, or in the Lachnidae, we can assume that these groups are attacked by a strictly specialized parasite complex. On the contrary, in the Aphidoid aphids, we can expect a broad spectrum of parasites to occur, with a high probability of successful unnatural host propagation. Naturally, host specificity influencing factors and the evolutionary aspect must be used as a basis of such predictions.

REFERENCES. 27, 99, 111, 112, 131, 141, 142, 144, 191, 225, 234, 238, 240, 282, 301, 306, 308, 339, 342, 450, 452, 454, 455, 456, 461, 476, 479, 511, 523-32, 536-7, 551, 570, 580-5, 613, 615, 618, 649, 650, 693, 697, 700, 705, 719, 721, 758, 792, 809-14, 817, 821, 846, 861, 862, 863, 902-3, 905, 919, 920, 932, 954, 975-88, 996, 1003, 1005, 1011, 1013, 1110, 1112, 1114, 1115, 1116, 1137, 1135-7, 1189, 1256, 1266, 1288, 1290, 1341-2.

Unnatural Host Propagation

Research on host specificity, distribution and effectiveness of the parasites has shown that certain aphid groups are not attacked by the parasites at all, or they are attacked to a low degree, or there may be different groups of parasites attacking the same aphid species in various parts of the world, or the effectiveness of the parasites is low, etc. This state of research has led to the trend, which is also commonly applied in other groups of entomophagous insects, when various hosts—so called unnatural hosts—are propagated as new hosts to certain parasite species and various methods have been used to put such aphids into the host range of a given parasite species. The main idea of unnatural host propagation is to find parasites capable of attacking and successively parasitizing the pest aphids, although their natural host need not be a pest species. It is necessary to note that unnatural host propagation is a state of research, where the host-specificity of separate species must be known to avoid the propagation of an unnatural host which later would be found to be a natural one in reality.

— REVIEW. It is an aim of this review to show on the one hand, the development of research of unnatural host propagation in aphid parasites, and, on the other hand, the rather unsatisfactory level of our contemporary knowledge.

TELENGA (1950): when studying the significance of aphid locomotion with respect to parasite attack, he recognized *Lysiphlebus fabarum* failed to oviposit in young nymphs of *Dactynotus picipidis* as the latter escaped before the parasite was able to insert its ovipositor, many attempts of this kind having been observed. There is no doubt that *D. picipidis* is a member of an aphid group that is known to be rarely parasitized by the mentioned parasite species in nature, although we ourselves know of such cases (see: MACKAUER & STARY, 1967); the aphid would not represent an unnatural host in this respect. Moreover, it is not apparent whether the failure in parasite oviposition was due to laboratory conditions or whether it was seen just on the host plant where the aphids were feeding in the field. According to our observations,

young instars of *Dactynotus* species exhibit less defensive movements and escape reactions than the higher instars or adult aphids; the parasite, though known to be very slow in oviposition, would perhaps be able to oviposit successfully while undoubtedly being unable to insert its ovipositor and oviposit into a moving low instar aphid nymph.

GEORGE (1957) made experiments with propagation of various aphids attacking field crops and their parasites to show the existing host range. Some experimental host aphid combinations can be classified as unnatural host propagation too. Besides obvious cases of parasite behaviour to unnatural hosts (disregarding), *Myzus persicae* was found to be attacked by *Diacretiella rapae* in the laboratory (greenhouse), however, such a relationship was not observed in the field. It would appear that *Myzus persicae* was successfully propagated as an unnatural host under laboratory conditions. However, the aphid is known to be commonly attacked by the parasite mentioned in various parts of the world, including large areas of Europe. Therefore, a peculiar strain of the parasite may occur in Gr. Britain.

SCHLINGER, HAGEN & V.D. BOSCH (1960): *Trioxys pallidus* was successfully introduced as an agent in the biological control of *Chromaphis juglandicola* in California. The parasite attacks the aphid commonly in Europe, Asia Minor and C. Asia besides other species of dendrophilous Callaphididae. However, an unnatural host, *Tinocallis caryaefoliae*, an indigenous aphid pest on pecan (hickory) in California, was successfully propagated both in insectary and in the field. Experiments with *Monellia* species, another indigenous Callaphidid in California, were also made. The host range of *Trioxys pallidus* seems to be wide enough to include also some Callaphidid aphids which could not naturally be parasitized except in cases of parasite introduction into a given country.

GRIFFITHS (1960, 1961): Both papers seem to be of basic significance for unnatural host propagation research. His work was performed on *Monoctonus erepdis*, a parasite of the *Nasonovia* species, *N. ribisnigri* on lettuce being used as a natural host in the experiments. Detailed observations on the relationship of the parasite to its natural host were carried out, oviposition behaviour, host selection, defensive reactions of the host and factors influencing them were stressed most, immunity reactions of the host also being carefully dealt with. After the natural conditions of host-parasite relationship had been established, other lettuce and non-lettuce aphids were used in parallel experiments. Rather significant differences in various aphids with respect to the original natural state of host-parasite relationship were found. At the time when the experiments were made, there was still a rather poor knowledge of host specificity of the aphidid parasites in general if compared with recent years. For this reason, the relation of unnatural hosts by GRIFFITHS was made more or less by chance in many cases (non-lettuce aphids namely). This feature of work naturally does not change anything as to its value, and it would be an interesting research theme to apply a modern viewpoint on host-specificity in the experimental program initiated by GRIFFITHS.

EVENHUIS & DE JONG (1961): when dealing with the aphids and parasites on apple, these authors made certain experiments on host specificity of separate parasite species. They were unable to infest *Aphis pomi* with parasites of *Dysaphis plantaginea* on apple. Further research on this theme (see: EVENHUIS, 1962) has partially elucidated the problem.

V.D. BOSCH, SCHLINGER & HAGEN (1962) made further experiments (conf. SCHLINGER, HAGEN & V.D. BOSCH 1960) with *Trioxys pallidus*. According to earlier observations *Monellia costalis* was parasitized by *Tr. pallidus* only in laboratory rearings and in cages in the field. However, later field observations have shown that even *M. costalis*

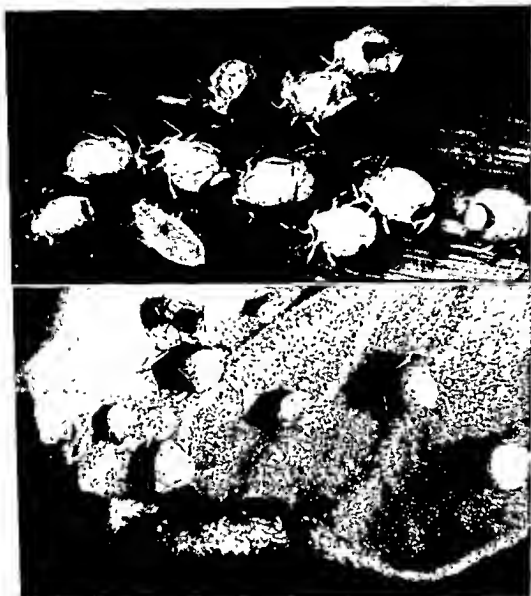


Fig. 260. Unnatural host propagation. Above: *Aphidius transtaspicus* as a parasite of *Hyalopterus pruni* on *Phragmites communis* (natural host, field). Below: *A. transtaspicus* reared on *Aphis craccivora* on *Vicia faba* (unnatural host, laboratory).

and *M. caryae*, species closely related to *Chromaphis juglandicola*, were found to be free from the parasite. This is an excellent example of the difference between laboratory and field environments with respect to unnatural host propagation, some still unknown factors occurring in the field that seem to restrict *Tr. pallidus* to *Chromaphis juglandicola*, the *Monellia* species being omitted.

STARÝ (1964): During the research on the biology of *Aphidius megourae*, a parasite of *Megoura viciae*, experiments were made to propagate *Acyrthosiphon pisum* as the unnatural host as the parasite seems to be an effective but unfortunately a strictly specialized species, its natural host being of low economic importance.

STARÝ (1966) has summarized certain aspects on unnatural host propagation in aphid parasites.

WILBERT (1967) dealt with the propagation of *Neomyzus circumflexus* and *Rhopalosiphum ascalonicus* as unnatural hosts of *Diaeretiella rapae* in the laboratory. The im-

munity responses of aphids against the parasite were observed to be specific. The apparently less developed mechanical defensive reactions were classified as being equivalent to strong physiological immunity reactions.

STARÝ (unpublished) made experiments on unnatural host propagation using *Aphidius transcaspicus* as a parasite. This parasite normally attacks *Hyalopterus pruni* and *Longiclavus donacis* over its distribution area. Nevertheless, it was necessary to try to propagate new laboratory hosts to rear the parasite in masses because of a biological control program, the natural hosts being reared in the laboratory with certain difficulties. During the unnatural host propagation experiments *Aphis fabae* and *A. craccivora* were found to be useful, the latter host being then used in mass-rearing of the parasite and applied also to a host in artificial foci unit methods in a biological control program in Czechoslovakia. Parasite material reared originally from *H. pruni* both in the field and laboratory, and later on *A. craccivora* in the laboratory, was found to be reversible in action, i.e. the parasites reared for many generations on *A. craccivora* in the laboratory were able to attack and successfully parasitize *H. pruni* when liberated in the field (Fig. 260). The above experiments were based on the knowledge of the basic peculiarities of parasite host specificity. They show, simultaneously, the significance of unnatural host propagation for a biological control program.

STARÝ (unpublished) also propagated *Aphis craccivora* as the unnatural host of *Diaeretiella rapae*, a parasite of *Brevicoryne brassicae*, in the laboratory. Only F_1 progeny was observed to develop completely, further progeny not being produced owing to unknown reasons. The unnatural host mentioned is believed to be near or possibly also in the natural host range of the parasite.

- List of parasite species. All the records on parasite species used in unnatural host propagation are mentioned in this list irrespective of whether the propagation was successful or not. Detailed records can be found in the papers mentioned below.

Aphidius matricariae: *Brevicoryne brassicae*—GEORGE 1957.

Aphidius megourae: *Acyrtosiphon pisum*—STARÝ 1964.

Aphidius transcaspicus: *Acyrtosiphon pisum*—STARÝ (unpublished), *Aphis craccivora*—STARÝ (unpublished), *A. fabae*—STARÝ (unpublished), *Megoura viciae*—STARÝ (unpublished).

Diaeretiella rapae: *Aphis craccivora*—STARÝ (unpublished), *A. fabae*—GEORGE 1957, *A. nasturtii*—GEORGE 1957, *Macrosiphum rosae*—GEORGE 1957, *Neomyzus circumflexus*—WILBERT 1967, STARÝ (unpubl.), *Rhopalosiphum arvalis*—WILBERT 1967.

Lysiphilus fabarum: *Brevicoryne brassicae*—GEORGE 1957, *Dactynotus picridis*—TELENGA 1950.

Monoctonus crepidis: *Aphis* sp. (on *Epilobium*)—GRITTIS 1960, *Aulacorthum solani*—GRITTIS 1960, *Brachycaudus helichrysi*—GRITTIS 1960, *Macrosiphum euphorbiae*—GRITTIS 1960, *Myzus persicae*—GRITTIS 1960, *Nectarosiphon rubi*—GRITTIS 1960, *Neomyzus circumflexus*—GRITTIS 1960, *Sitobium avenae*—GRITTIS 1960, *Sitobium fragariae*—GRITTIS 1960.

Trioxys pullidus: *Monellia costalis*—V. D. BOSCH, SCHLINGER & HAGEN 1962, *Timocallus caryacfoliae*—SCHLINGER, HAGEN & V. D. BOSCH, 1960.

- List of aphid species. All the records on unnatural host propagation are mentioned in this list irrespective of whether the propagation was successful or not. Detailed records are given in the review below:

Acyrtosiphon pisum *Aphidius megourae*—STARÝ 1964, *A. transcaspicus*—STARÝ (unpubl.).

Aphis craccivora *A. transcaspicus*—STARÝ (unpubl.), *Diaeretiella rapae*—STARÝ (unpubl.).

Aphis fabae *Aphidius transcaspicus*—STARÝ (unpubl.), *Diaeretiella rapae*—GEORGE 1957.

Aphis nasturtii *Diaeretiella rapae*—GEORGE 1957.

- Aphis ponsi*: Parasites of *Dysaphis plantaginea*—EVENHUIS & DE JONG 1961.
Aphis sp. (on *Epilobium*): *Monoctonus crepidis*—GRIFFITHS 1960.
Aulacorthum solani: *Monoctonus crepidis*—GRIFFITHS 1960.
Brachycandus helichrysi: *Monoctonus crepidis*—GRIFFITHS 1960.
Brevicoryne brassicae: *Aphidius matricariae*—GEORGE 1957, *Lysiphlebus fabarum*—GEORGE 1957.
Dactynotus picridis: *Lysiphlebus fabarum*—TELENGA 1950.
Macrosiphum euphorbiae: *Monoctonus crepidis*—GRIFFITHS 1960.
Macrosiphum rosae: *Diaeretiella rapae*—GEORGE 1957.
Megoura viciae: *Aphidius transcaspicus*—STARÝ (unpubl.).
Mouellia costalis: *Trioxys pallidus*—V. D. BOSCH, SCHLINGER & HAGEN 1962.
Myzus persicae: *Monoctonus crepidis*—GRIFFITHS 1960.
Nectarosiphon rubi: *Monoctonus crepidis*—GRIFFITHS 1960.
Neomyzus circumflexus: *Diaeretiella rapae*—WILBERT 1967, STARÝ (unpubl.), *Monoctonus crepidis*—GRIFFITHS 1960.
Rhopalomyzus ascalonicus: *Diaeretiella rapae*—WILBERT 1967.
Sitobium avenae: *Monoctonus crepidis*—GRIFFITHS 1960.
Sitobium fragariae: *Monoctonus crepidis*—GRIFFITHS 1960.
Tinocallis caryaefoliae: *Trioxys pallidus*—SCHLINGER, HAGEN & V. D. BOSCH, 1960.

TRENDS. Various trends can be followed in unnatural host propagation:

1. Laboratory propagation. An unnatural host is being parasitized by a ♀ parasite under laboratory conditions. These conditions permit the change or at least modification of the environment purposely in many ways.

This research trend was mostly accepted by various authors.

2. Propagation in a greenhouse. Indigenous parasites may be used accidentally or purposely in aphid control in greenhouses. However, in greenhouses, an indigenous parasite can find a new host, besides the host controlled, and due to the pressure of restricted environment, it may attack and successfully parasitize it, although the aphid would never be attacked by the parasite in the field, being dependent on greenhouse conditions exclusively (tropical species.) Example: In Czechoslovakia, we have used experimentally *Diaeretiella rapae* as a control agent against *Myzus persicae* in a greenhouse. However, another greenhouse aphid—*Neomyzus circumflexus*—a typical species of tropical origin, was also rarely attacked and successfully parasitized.

3. Field propagation. A parasite species may be purposely introduced to control certain pest species in a given country. However, it may include also some new, alternative hosts, which otherwise would not be parasitized due to the existence of a certain barrier in the parasite distribution area. Example: *Trioxys pallidus* was introduced into California to control *Chromaphis juglandicola*. This aphid is its natural host in Europe, Asia Minor and C. Asia. However, in California, it accepted also another host—a new alternative host—*Tinocallis caryaefoliae*, an indigenous Californian pest on Pecan. Although the aphid was originally propagated in the laboratory, there seems to be no doubt that it would be accidentally parasitized in the field too.

4. Artificial parasitization means an implantation of a parasite egg or larva into an aphid. In this case, no natural oviposition occurs. In aphid parasites, implantation of a parasite egg was mostly applied, while implantation of parasite larvae does not seem to be used.

5. Rearing on synthetic food. Synthetic food seems to be well grouped as a certain kind of unnatural host as we have to classify it as a "host" in host-parasite relations.

No attempts to rear aphid parasites on synthetic food are known in the literature.

With respect to synthetic food, there seem to be two possible trends as to the unnatural host propagation:

1. Mass rearing of aphids on synthetic food and successive propagation of parasites. Rearing of aphids on synthetic food is widely used in some countries. The successive propagation of parasites might be useful in mass-rearing of parasites to avoid the factor of host plant, as the latter may cause seasonal troubles in obtaining such material.

2. Direct rearing of parasites on unnatural food. This trend seems to be more of a theoretical value with respect to the ascertainment of the composition of parasite food, etc. Such experiments usually are started with transferring a parasite egg into a given medium, so that all the factors connected with host-specificity of the parasite are almost excluded.

— SELECTION OF HOST AND PARASITE. A careful selection of material for unnatural host propagation is the first necessary step. Generally, we start with the evaluation of a given parasite species that is to be propagated to an unnatural host (pest aphid), or we may start with the pest aphid and try to select parasite species as agents in unnatural host propagation.

The knowledge of host-specificity of parasites and factors that influence it is the basis in both cases. The host range must be known in the parasite species to have a general idea as to the taxonomy and ecology of its host aphids, about its occurrence in various habitats and microhabitats, etc. Naturally, geographic distribution is also important in case the parasite has to be introduced and colonized in a given country. From this point of view the given unnatural host must be evaluated and compared with the natural host of the parasite. It is evident that such a comparison will cause a restriction of some aphid groups at least. For example, we should hardly try to use a parasite species in unnatural host propagation on Adelgoid aphids, as this group is not parasitized by the aphidiids at all. Similarly, we should never use parasites of Cinarine aphids, of Callaphidid aphids, etc., on other aphid groups as these parasites represent mostly strictly specialized groups that do not parasitize other aphids. On the contrary, parasites of other aphids may cover several aphid groups in their host range, taxonomy and ecology of the aphids playing a different role as to their importance. Relatively widely specialized parasites seem to be more useful in unnatural host propagation, while more strictly specialized species will be useful in unnatural host propagation experiments using their closely related aphids only. As to the former case, we can expect that e.g. *Lysiphlebus fabarum* will attack various *Aphis* species and a number of other groups in unnatural host propagation as well due to its wide natural host range. *Troxys pallidus*, on the other hand, can be expected to attack only some dendrophilous Callaphidid aphids due to its relatively strict range.

Similarly, a pest aphid belongs to a certain group of aphids. We must first of all evaluate the composition of its natural parasites to know whether they are mostly strictly specialized to this group, or whether their host range is wider, etc. Parasite-agents in unnatural host propagation are best found in parasite complexes attacking the species or groups related to the pest, various faunistic complexes being rather helpful in this respect.

After the species of host or parasite is preliminary selected to be used in unnatural host propagation, more detailed research is undertaken to show the true relation between these organisms.

— Techniques. Unnatural host propagation experiments need a good deal of knowledge of the various peculiarities in host-parasite relationship. We have tried to mention here at least some of them.

— Manipulation of parasite adults. Many parasites do oviposit in unnatural hosts

as well, without any peculiar behaviour. In such a case, there is no need of manipulating parasite adults except for the usual manipulating of environment in a corresponding way (see: Oviposition). However, it is necessary to mention the well known fact that oviposition by a parasite is not necessarily an index to host suitability (BEES, 1939).

In some parasites, the ♀♀ do not oviposit in the unnatural host aphids, either ignoring them almost completely, or tapping them with antennae, or exhibiting a preoviposition behaviour, the oviposition not taking place, however. All these features mean that there are some factors which prevent the ♀ from ovipositing. Therefore, the parasite ♀ must be manipulated in a certain way to try to stimulate its oviposition in the unnatural host.

Under natural conditions there is no difference between mated and unmated ♀♀ as to the oviposition. A similar behaviour can be expected to occur in cases of unnatural hosts as well.

Younger ♀♀ are known to oviposit more readily than the older ones. Water and food (honey) are further necessities. A parasite ♀ must be supplied with water and honey before the experiment is started, otherwise its oviposition stimuli are soon overruled by searching for water and later for food and oviposition is broken or less intensive in consequence.

Temporary absence of host aphid seems to be a very strong stimulus for a parasite ♀. One day's absence of host aphids, in the presence of water and honey, is usually enough for parasite ♀♀ to try to oviposit in each other, in empty mummies, etc. In consequence, they can also readily oviposit into unnatural hosts when added to parasite rearing cages.

The possibility of ovipositing in a single host aphid species with no preference possibility may be a strong stimulus to a parasite ♀. Sometimes it is necessary to mix (see below) the natural and unnatural host species to stimulate the parasite oviposition through the natural host, unnatural host being also attacked in sequence.

In case of lack of suitable host instars the ♀♀ usually oviposit in the instars available. In this way, a selected instar of an unnatural host can be infested by a parasite.

As the original mummies from which the ♀ parasites have emerged may have a certain role in host selection through odour, etc., it is recommended to take them out of the rearing cages, ♀♀ only being present in the cage with a supply of water and honey.

- Manipulation of host aphid. The unnatural host aphid, being a part of the parasite environment, must also be dealt with in a similar way.

A host aphid must sit and suck in the usual way on its host plant, such as a piece of leaf, stem, etc. To take aphids away from their host plants and put them into Petri dishes makes them move and search for food, and represents an unsuitable factor for parasite searching or oviposition. Aphids are more easily attacked by a parasite when sitting and feeding on a plant; at least, it takes some seconds before they can escape as they must take out the rostrum from the plant tissues. Aphids reared in laboratory conditions, where there are weaker various stimuli such as movements of plants by wind, rain, etc., usually exhibit much more reactivity than under field conditions. Temperature in a rearing room is important, the aphids being less reactive under temperatures below their ecological optimum and more reactive if the temperature is higher.

In some cases, mixed populations can have a stimulatory effect as to the attack on unnatural host, in other cases the parasites carefully select the natural host and omit the unnatural one (see: STARÝ, 1964, GRIFFITHS 1960, 1961, GEORGE 1957, etc.).

In certain cases, high density of unnatural host may cause its parasitization, although

such hosts are normally omitted. Such cases are known to occur in natural conditions, the hosts naturally then being classified as occasional rather than as unnatural ones. EVENHUIS (1962) observed that *Aphis pomi* is attacked by parasites attacking *Dysaphis*-species on apple only in case it is rather common. A similar microhabitat, i.e. leaf-curling, in this case is a result of *Aphis pomi* high occurrence, and it is believed to be also of importance. SCHLINGER & HALL (1960) found *Aphis helianthi* and *Myzus persicae* to be rarely attacked by *Lysiphlebus testaceipes* in California. It is believed possible that both the species mentioned are attacked commonly by this parasite only when in company with a more preferred host *Aphis gossypii*. Another example observed is that of *Aphis spiraeola* and the parasite mentioned. The parasite is stimulated to oviposit in this aphid by the presence of a suitable host, *Toxoptera aurantii*, nevertheless, the parasite failed to develop completely in *A. spiraeola*. It is apparent that similar conditions might be created in the laboratory conditions in order to favour the unnatural host.

Where the natural and unnatural hosts are different in mobility, it is possible to make the mobility of one species lower through its transfer into colder temperature for some time, or to use a slight anaesthetization by CO₂. This material must then be used quickly before these temporary influences disappear. This method is useful in lowering the mechanical defensive reactions of an unnatural host aphid (STARÝ 1964).

Different instars of an aphid are known to reveal a somewhat different behaviour. Usually, higher instars are more sensitive to parasite attacks and exhibit stronger mechanical defensive reactions. For this reason, the most suitable instar must be selected for unnatural host propagation.

Sublethal doses of insecticides might lower the immunity reactions of an unnatural host aphid.

- *Microhabitat*. A microhabitat is often known to be of great importance as one of the factors determining the host range of parasites in nature. One host species may be attacked in one microhabitat and ignored in another by the same parasite. For this reason, microhabitat conditions must be created so as to be closely similar both for natural and unnatural hosts. It must be stressed that also the kind of aphid colony, whether it is scattered or dense, can be important, the same as shady or open places on plants, etc.

- *Parasite stages*. A parasite egg seems to be the most suitable parasite stage to be transferred into unnatural host body. Whether oviposited by a ♀ or injected, its transfer is not connected with remarkable influences on the host integument. However, the egg represents also a parasite stage which can be very easily destroyed by the host through immunity reactions. Eggs can be obtained through the dissection of parasite ♀ reproductive organs, where they are usually found in a larger number if there was no oviposition chance given to the ♀ for about a day before dissection. Aphids are usually anaesthetized with moistened CO₂ when the parasite egg is injected.

A parasite larva may also be transferred. This method for the time being is only of a theoretical value but, in our opinion, it might show certain new relations with respect to unnatural host propagation as the host might exhibit less or a weakened immunity to living parasite larvae of different stages than to an egg or parasite embryo that starts to develop inside its body. Parasite larvae of different stages can be obtained through dissection of various host aphids. Special techniques must naturally be developed (washing of the larvae dissected in physiological solution, etc.).

Pupa, as well as last instar larva, is found inside the dead mummified aphid, so that it does not have direct significance in unnatural host propagation. Perhaps, the

situation of mummified—natural hosts among the living unnatural host aphids could have a certain significance.

The behaviour of parasite adults with respect to unnatural host propagation is of basic significance. Searching behaviour, preference of host species and host instars, oviposition behaviour, etc., is all of great importance, representing the relatively most natural part in an unnatural host propagation program. It seems probable that if there are strong adverse reactions of a parasite ♀ to an unnatural host, it will be difficult to acquire success, although the implantation of parasite developmental stages into the host body may be successful, as the latter case does not occur in nature.

— *Transferring of parasite developmental stages.* Principally, three ways of transferring parasite stages into an unnatural host must be recognized:

1. Oviposition by parasite female. In many cases, ♀♀ readily oviposit into an unnatural host. This feature makes the transference of a parasite egg inside the unnatural host body quite easy, however, care must be taken to ascertain whether the ♀ did actually lay an egg. To recognize whether or not an egg was laid, special methods were developed. These are either microscopical (GRIFFITHS 1960, 1961), or through radioactive labelling. The latter method was used by GEORGE (1957); there were no positive counts, however, as the level of contamination by radio-phosphorus deposited in the egg was not sufficient to be detectable.

2. Injection of parasite egg. In case there is no natural oviposition into an unnatural host, it is necessary to transfer the egg into the host's body in an artificial way. Eggs are usually injected into the abdominal parts of the aphid body as these are the most suitable for natural oviposition too; there are only some exceptions when the parasites deposit their eggs into a certain restricted part of the host's body (nerve tissues).

3. Implantation of parasite larva. In some cases, parasite larva can be implanted into the unnatural host aphid body.

— *Single parasitism, superparasitism and multiparasitism.* Experiments on the influence of parasitization in different instars of alate and apterous aphid nymphs have shown that there is a different influence of single and superparasitism (JOHNSON 1959). This might also mean that superparasitism (and multiparasitism) might also reveal different effects in unnatural host propagation than single parasitism.

A similar case seems to represent the sequence of attack by parasite ♀♀, whether it is simultaneous or gradual, if simultaneously or gradually several eggs are or are not laid, whether this is done by parasite ♀♀ of a single or different species, etc.

— *REACTIONS OF THE HOST.* Host resistance in its recent appearance is a result of the evolution of host-parasite relations. It originated in ancient periods of evolution of both groups, as this evolution was not parallel due to various changes and different responses of both groups to environment, today's relations disclose quite a number of different features that are also different in separate groups or species. The modern viewpoint on parasitism with respect to natural limitation keeps parasitism as useful for host aphid, as parasites (and other natural enemies) limit the population of the aphid in the frame of community equilibrium, protecting thus on the one hand the existence of the community, and on the other hand, preventing the aphid species from overpopulation with resulting destruction of food sources that could mean the elimination of the species occurrence in the area. As a result of this process, various degrees of specificity to different hosts have developed among the parasites. The host range of parasites attaches them more or less to a certain community and prevents the other parasites from taking part in the host-parasite relationship. Naturally, such relations are only relatively constant, they develop in a similar way as the whole community.

Today, the resistance to parasites can be observed in two main directions:

1. Mode of parasite attack. It is a reaction of the parasite ♀ to the host. It is rather complicated, starting with the habitat finding, host finding, host suitability and host acceptance, that result in the final act—the oviposition of an egg into the host's body; however, such complicated oviposition may not mean real suitability of the host for parasite development (see: BESS 1939). This feature may seem perhaps somewhat strange, however, as in adult behaviour it is believed to result possibly in new host parasitization and a wider host range.

A parasite ♀ attack is successful in case the physical (mechanical) reactions of the host to the attack are not too strong. The host-parasite relationship, resulting in more or less parasite adaptation to the host's behaviour, is the determining factor.

2. Reaction of the host to parasite developmental stages. The next feature of host-parasite relationship is the reaction of the host aphid to the presence of parasite developmental stages. This reaction is much more selective in action than oviposition of the parasite.

— *Factors of host resistance.* Physical factors include on the one hand the morphological-anatomical peculiarities of the host aphid (pubescence, integument, wax covers) as well as defensive responses of the host to an attack of the parasite.

Chemical factors include such features as odour, food-competition, etc.

Physiological factors, such as immunity reactions are included in this group, (cellular or humoral encapsulation). Phenological factors include peculiarities in the seasonal occurrence of aphids.

All these factors are covered by the external environment, which plays the primary role in parasite specificity and naturally in host resistance as well.

— *Reactions of the host to different parasite stages.* Reactions of the host aphid to the attack of the parasite may principally be passive through the presence of various wax covers, etc., or active, such as an active defence against the attack through the movements of legs, running away, falling down from the plant, etc. In unnatural host propagation, the mode of parasite attack must be carefully observed in the natural host and compared with that of the unnatural host as this is the factor that will basically determine the first phase acceptance of the new host in the laboratory or field conditions.

Observations of various authors have shown that there are generally two kinds of reactions of the host to the egg or parasite larva:

1. Cellular reaction—encapsulation. In this kind of reaction the products of the blood cells of the aphid encapsulate the parasite embryo and isolate it from the supply of food and oxygen. Encapsulation was observed in the propagation of *Monoctonus crepidis* on *Neomyzus circumflexus* (GRIFFITHS 1961) and in *Diaeretiella rapae* on *Rhopalosiphum ascalonicus* and partially on *Neomyzus circumflexus* (WILBERT 1967) (Tables 9-10).

2. Humoral reactions. In this case, the parasite embryo is influenced by chemical secretion inside the host's body. Humoral reaction is known to occur probably in the propagation of *Monoctonus crepidis* on *Aulacorthum solani*, *Macrosiphum euphorbiae* and *Myzus persicae* (GRIFFITHS 1961) (Fig. 261-262).

— *Degeneration processes in parasites.* These processes were examined in a comparative way by GRIFFITHS (1961), who found that the rate at which these processes start to appear and the stage which the parasite reached before they set in vary in different species and also in different individuals of each species. Eggs of *Monoctonus crepidis* were ascertained to develop in *Macrosiphum euphorbiae* and *Neomyzus circumflexus* vigorously to the 24-hour stage, in *Myzus persicae* and *Aulacorthum solani*, however, the development was arrested at an earlier stage (Fig. 261-262).

In unnatural host propagation, it is rather important to know the intensity and

occurrence of degeneration processes in order to establish the degree of host immunity to a certain parasite.

— *Relations between host reactions.* WILBERT (1967) noticed that in the case of propagation of *Rhopalomyzus ascalonicus* and *Neomyzus circumflexus* as unnatural hosts of *Diaeretiella rapae* both the aphids exhibited relatively low mechanical reactions (encapsulation). According to WILBERT's opinion, which seems to be well justified, there occurs apparently a certain compensation between the intensity of various kinds of reactions: in the case mentioned, mechanical reactions are low because of strong physiological reactions (Tables 9-10).

— *Influence of host resistance on parasite.* Host resistance generally results in the host range of a parasite species. However, as is known, in this host range the true hosts of the parasite are included, i.e. such hosts that do not show resistance to the parasite in favourable environments in the parasite distribution area. However, various features such as geographic distribution have caused that there occur also so-called potential hosts, that might also be successfully parasitized by the parasite and fall within its host range if they were not separated in nature. Unnatural host propagation, therefore, may deal either with the study of how to overcome the resistance of certain hosts, or, on the other hand, to search for a potential host of various parasites.

— *PARASITE ADAPTATION.* Parasite adaptation to an unnatural host may be relatively irreversible or reversible. In the case of an irreversible adaptation, a strain or race is developed under laboratory conditions that does not attack or at least does not prefer the natural host both in the laboratory and field conditions. For the time being, we are not aware of any examples of such adaptation occurring among the aphidiids. In the case of reversible adaptation, the adaptation of a parasite population on an unnatural host is only temporary and the parasite again attacks the natural host if it has a chance to do so, the unnatural host may or may not be attacked if given a chance of selection. We can mention several examples, such as *Trioxys pallidus*—*Monellia costalis* and *Tinocallis caryaefoliae*, *Aphidius transcaspicus*—*Aphis craccivora*, etc.

Host acceptance and suitability best show the degree of parasite adaptation to an unnatural host. Several cases are recognized:

1. The host is entirely ignored by the parasite. There is neither oviposition, nor development of the parasite in the host (see: GEORGE, 1957).

2. The host is partially ignored by the parasite; occasionally, eggs may be deposited, but development does not occur (see: GEORGE, 1957, STARÝ, 1964).

3. The host is accepted by the parasite. There is oviposition, but development of the parasite does not follow due to strong immunity reactions of the host (see: WILBERT, 1967).

4. The host is accepted by the parasite. Oviposition occurs. There is an incomplete development of the parasite; it usually dies during larval development (see: GRIFFITHS, 1961).

5. The host is accepted by the ♀, oviposition occurs. There is a complete development in a part of the parasite population, and incomplete development in another (see: WILBERT, 1967).

6. The host is accepted by the ♀, oviposition occurs. The development is normal under laboratory conditions. Example: *Aphidius transcaspicus*—*Aphis craccivora*, *A. fabae*.

7. The host is accepted by the ♀. Oviposition occurs. The development is normal under laboratory conditions and in the field, the host, however, is not attacked under field conditions except when caged. Example: *Trioxys pallidus*—*Monellia costalis*.

8. The host is accepted by the ♀. Oviposition occurs. The development is normal both under laboratory conditions and in the field. The host is attacked both in the laboratory and in the field. Example: *Trioxys pallidus*—*Tinocallis caryaefoliae*.

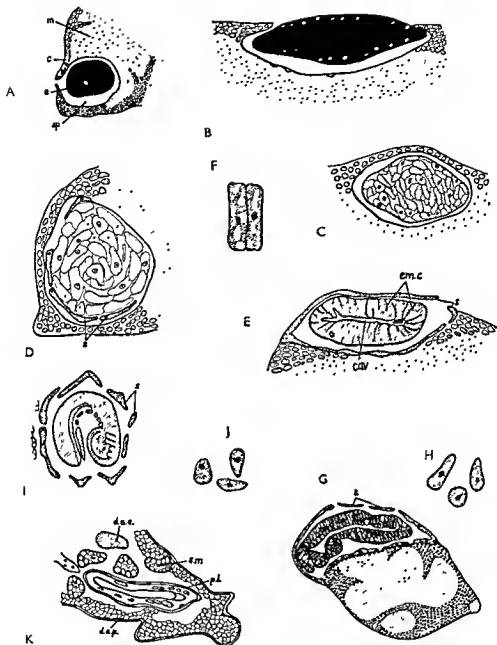


Fig. 261. Development of *Monocotylus crepidus* (= *paludum*) in its true host, *Nasonovia ribis-nigri*. A - immediately after attack, c - nerve tissue cortex, e - parasite egg, m - nerve tissue medulla, sp. - space separating parasite from nerve tissue of host. B - 6 hours after attack. The nuclei can be seen around periphery of the egg. C - 11 hours after attack. The cytoplasm has by now divided to produce a segmented embryo. D - 17 hours after attack. The scrota (s) can be seen separating off as a flattened layer of cells to the outside of the embryo. E - 20 hours after attack. The scrota (s) surrounds an embryo which consists of columnar cells (em. c) arranged about a central cavity (cav). F - ditto, columnar embryo cells. G - 36 hours after attack. The parasite embryo has now come to lie adjacent to the nervous tissue, suspended in the sac-like scrota (s). The central cavity is now surrounded by a layer of cells 2 to 3 cells deep. H - ditto,

No.	Aphid species	No. of aphids	dissected	No.	%	Parasitized aphids	
						No.	
						normal larvae	encapsulated eggs
1	<i>N. circumflexus</i>	70	70	56	80	2	87
	<i>M. persicae</i>	70	13	10	77	13	0
2	<i>N. circumflexus</i>	70	62	37	60	0	64
	<i>M. persicae</i>	70	26	25	96	41	0
Total	<i>N. circumflexus</i>	140	132	93	70	2	151
	<i>M. persicae</i>	140	39	35	90	54	0

Table 9. Encapsulation of larvae of *Diaretia rapae* by *Neomyzus circumflexus*. (WILBERT, 1967).

No.	Aphid species	No. of aphids	dissected	No.	%	Parasitized aphids	
						No.	
						normal larvae	encapsulated eggs
1	<i>Rh. ascalonicus</i>	50	43	33	77	0	57
	<i>M. persicae</i>	50	10	9	90	16	0
2	<i>Rh. ascalonicus</i>	50	40	6	15	0	6
	<i>M. persicae</i>	50	36	16	44	17	0
3	<i>Rh. ascalonicus</i>	40	31	10	32	0	11
	<i>M. persicae</i>	40	23	9	39	18	0
4	<i>Rh. ascalonicus</i>	100	50	29	58	0	48
	<i>M. persicae</i>	100	36	15	42	17	0
Total	<i>Rh. ascalonicus</i>	240	164	78	48	0	122
	<i>M. persicae</i>	240	105	49	47	68	0

Table 10. Encapsulation of eggs of *Diaretia rapae* in *Rhopalomyzus ascalonicus*. (WILBERT, 1967).

embryo cells at 36 hours. I - two days after attack. Parasite embryo lying in body cavity of host, surrounded by serosal envelope (s). J - ditto, embryo cells at two days. K - 2-3 days after attack. First-instar larva which has now freed itself of its serosa., d.a.e. - degenerating aphid embryo; d.a.p. - degenerating aphid adipose tissue; p.l. - parasite larva; s.m. - serosal mass (redrawn from GRIFFITHS, 1961).

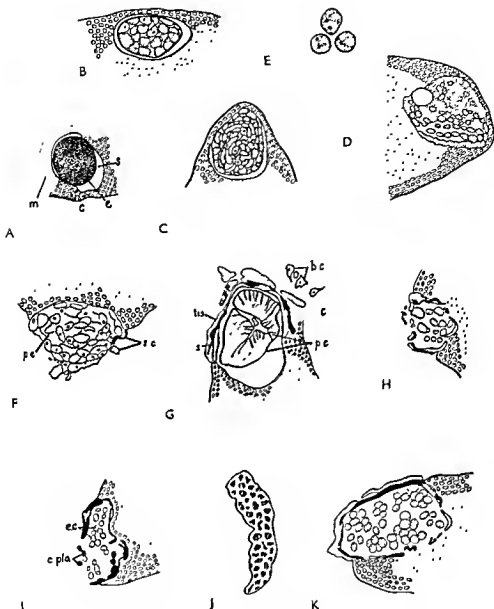


Fig. 262. Abortive development of *Monoctonus crepidis* (= *paludum*) in *Aulacorthum solani*. A - immediately after attack, c - nerve tissue cortex; e - parasite egg; m - nerve tissue medulla; s - space separating parasite from nerve tissue of host. B - 11 hours after attack. C - 24 hours after attack. D - 2-3 days after attack, Degenerating parasite embryo still lodged within nervous tissue of its host. E - ditto, parasite embryo cells in *Aulacorthum solani* at 2-3 days, showing vacuolisation of the cytoplasm and disorganisation of the nuclear material.

Abortive development of *M. crepidis* (= *paludum*) in *Neomyzus circumflexus*. F - 77 1/2 hours after attack, p.e. - segmenting parasite embryo; s.c. - scattered capsule tissue. G - 24 hours after attack. Development of capsule around parasite embryo, b.c. - blood cells of host; c - capsule, p.e. - parasite embryo; s - serosa of parasite; tis. - tissue formed by coalition of blood cells of host. H - 36 hours after attack. The capsule has by now spread around so as to enclose, almost completely, the embryo, which has not increased at all in size over the 24-hour condition. I - two days after attack. The

For the time being, we have rather poor information on possible changes in parasite bionomics and ecology. For example, we have observed different egg dispersal in *Aphidius transcaspicus*, when ovipositing in the unnatural host, *Aphis craccivora*, this being probably a feature caused by different aphid responses to parasite attack than in the natural host, *Hyalopterus pruni*.

There is no doubt that there will necessarily be a number of parasite adaptations to the unnatural host biology in the field also.

— LABORATORY AND FIELD ENVIRONMENTS. Laboratory conditions enable us to control the environment in various ways with respect to unnatural host propagation. As to the host specificity phases, at least host habitat finding and host finding may well be replaced through laboratory conditions, the other phases being possibly modified in some way. The creation of favourable conditions in the laboratory may result in successful propagation of a host aphid as an unnatural host of a given parasite. We know today a number of such examples and they will be more numerous after further research is undertaken.

As we have mentioned above, unnatural host propagation can be basically directed into two ways: First, an unnatural host is propagated for laboratory purposes such as mass-rearing, etc., and, second, an unnatural host is to be attacked by a parasite both in the laboratory and in the field. In the latter case, results obtained in field conditions are the only ones that may show whether unnatural host propagation was successful or not. An illustrative example is mentioned by v.d. BOSCH, SCHLINGER & HAGEN (1962): Two unnatural hosts of *Trioxys pallidus*, an introduced species in California, were propagated, i.e. *Monellia costalis* and *Tinocallis caryaefoliae*. The first species was successfully propagated under laboratory conditions and in the field only if caged, it was, however, attacked by the parasite in the open. The second aphid was successfully propagated as an unnatural host both in the laboratory and in the field.

— BIOLOGICAL CONTROL. In certain trends of the biological control program the possible reversibility to natural host of a parasite reared on unnatural host is required. This is for instance if an unnatural host is used in parasite mass-rearing, where it serves only as a laboratory host. However, there is a well known tendency among parasites to develop strains preferring a host on which the given parasite population developed. In such a case, rearing of a parasite on an unnatural host could result in failing to parasitize its natural host when the parasites are liberated in the field. From the mentioned point of view, this parasite adaptation as to host preference must be avoided. If this tendency is ascertained, it would perhaps be the best to change the natural and unnatural host for a certain number of generations to rear on, to prevent development of unwanted host preferences in the parasite population reared.

In our experiments with *Aphidius transcaspicus*, a parasite of *Hyalopterus pruni* and *Longijunguis donacis* in nature, the parasite was found reversible when liberated in the field, although reared on *Aphis craccivora* for many generations in the laboratory. Or,

capsule now extends right around the degenerating parasite embryo, and small pieces of the capsule which have broken away during sectioning (c. pla.) are of about the same diameter as the cells which formed them; e.c. — degenerating embryo cells. J — ditto, a large piece of capsule material which has broken away and which shows the essential cellularity of its structure. K — four days after attack. Degenerating parasite embryo. There has been no change over the two-day condition and the embryo cells have not become shrunken (redrawn from GRIFFITHS, 1961).

another example of *Trioxys pallidus* in California can be mentioned (SCHLINGER, HAGEN & v.d. BOSCH, 1960). This parasite was reared, besides on its natural host *Chromaphis juglandicola*, on *Tinocallis caryaefoliae*, and was found to attack both hosts in the field.

In other cases, the irreversibility of parasite strains reared on an unnatural host is just required. This is, for example, the case of a parasite species used in unnatural host propagation, that are propagated on a new host—the pest aphid—although originally they attacked an economically indifferent species. The basic task of the unnatural host propagation here is to develop a relatively fixed preference for the new (pest aphid) host.

1. Propagation of effective parasites of economically indifferent aphids on pest aphids is a rather extensive trend and perhaps one of the most significant as to the future outlines of unnatural host propagation. Geographic distribution, the vicariance of species namely, might serve as one of the basic sources of selection of the material: species of various faunistic complexes are often known to attack related aphids, their introduction and propagation might be useful. Some examples may be found when comparing the specific composition and host specificity range of the parasites occurring in the complexes of the Far East and Europe.

2. Simultaneous control of several pests, natural and unnatural hosts, by introduced parasites. A wider host range of an introduced parasite species gives us a possibility to include new hosts in its host range in the country of establishment. For example, *Trioxys pallidus* was introduced into California as a control agent of *Chromaphis juglandicola*, an introduced pest aphid on Juglans, however, the parasite species was successfully propagated, both in laboratory and field, on *Tinocallis caryaefoliae*, an indigenous pest aphid on pecan (hickory) (v.d. BOSCH, SCHLINGER & HAGEN 1962).

3. Control of native pests by introduced parasites of alien species and genera. Native pest aphids can be generally controlled, as to the introducing of species, by other parasite species that attack the same host aphid in other countries, or by the parasites that attack alien aphid species or genera in another country. The latter trend in biological control is generally propagated by PIMENTEL (1963). Unnatural host propagation is necessary in the second case mentioned. Again, geographic distribution criteria (faunistic complexes) might be most helpful. More widely or rather widely specialized parasites seem to represent good subjects.

4. Alternative hosts of introduced parasites. It is well known, the absence of alternative hosts of introduced parasites represents one of the factors that may cause a failure in the permanent establishment of a parasite in a given country. Alternative hosts are rather important for a parasite species introduced to survive the possible periods of unfavourable conditions (temporary absence of its main host, etc.). Naturally, the host range of the parasite introduced and the composition of aphid fauna of the country are the basic factors that are important for unnatural host propagation. For example, *Aphidius smithi* was successfully introduced in California to control *Acyrtosiphon pisum*. Although this aphid is an inhabitant of perennial communities (alfalfa fields), which is useful for its occurrence, it would be more suitable if the parasite could find certain alternative hosts in the environment as well. In Czechoslovakia, where experiments on the establishment of *Aphidius smithi* have also been undertaken, we expect, so far as field experience shows, that the introduced parasite will attack various other *Acyrtosiphon* species in a similar way as the native parasite, *Aphidius ervi*, does. Unnatural host propagation in the laboratory could be helpful in case "unnatural host propagation" would not occur in field conditions in an accidental way.

5. Mass-rearing of parasites on an unnatural host is a commonly used practice in a biological control program in case the natural host is reared with difficulties, or in case the parasite is planned to be used in the control of its unnatural host in the field. For example, we have used successfully *Aphis craccivora* as unnatural host in laboratory mass-rearings of *Aphidius transcaspicus*, an introduced parasite to control *Hyalopterus pruni* in Czechoslovakia.

Besides the above mentioned significance in applied research, unnatural host propagation may be also classified as being useful for basic research. Degree of immunity reactions of unnatural hosts to different parasite species, unnatural range of host specificity of various parasite species, etc., all this is helpful in understanding the peculiarities of host specificity of parasites with respect to the evolution of the group as a whole.

REFERENCES. 46, 55, 80, 88, 129, 131, 151, 158, 241, 273, 290, 294, 305, 341, 346, 365, 450, 476-8, 499, 517, 552, 597, 605, 705, 740, 865-6, 896, 935, 966-7, 984, 1001, 1003, 1004, 1010, 1025, 1051, 1121, 1125, 1141, 1163, 1190, 1213, 1219, 1293, 1306.

Intraspecific Relations

The occurrence of a species in nature is regulated by a vast number of various factors, both internal and external. These phenomena are rather complicated and consequently we can deal only with some of them.

Internal relations within a parasite species seem to be the key position to the understanding of further relations of this species to the whole environment.

- VARIOUS DEVELOPMENTAL STAGES. Competitive relations among the parasite adults seem to be relatively rare. They can be observed commonly among the ♂♂, if they simultaneously try to mate the same ♀; however, the first ♂ that succeeds in tapping the ♀ with its antennae and climbing on its back is also usually the successful one in mating. Two or three ♂♂ may often be observed gradually climbing on the back of the first ♀ and trying to mate as well. This happens under conditions of high ♂ density, in laboratory rearings for example, otherwise, under natural conditions, several ♂♂ rarely try to mate the same ♀ simultaneously, as usually the first ♂ is successful and the once mated ♀ refuses to be mated for the second time by the same or other ♂♂. Therefore, such a competition among the adults is relatively rare in nature and it is completely lacking in deuterotokous and thelytokous species or populations, due to their mode of reproduction. Another kind of competitive relation seemingly occurs among the ovipositing ♀♀, when two or more ♀♀ try to oviposit the single host aphid simultaneously. However, according to our observations, such a case may be found practically in laboratory rearings under high parasite densities and even then the ♀♀ seem to ignore each other, the possibly adverse relations being overwhelmed by the ovipositional instinct. Competition could also take place among the parasite adults with respect to source of food, the honeydew, but the amount of honeydew present in an aphid colony seems to cover the necessary supply in nature.

According to observations of various authors no competitive relations seem to occur among the parasite eggs (see below).

Larval stage is the parasite stage in which the apparent competitive relations may be recognized with respect to parasite embryos or lower instar parasite larvae. This kind of competition is dealt with below (superparasitism) in detail.

In case of competition among several parasite developmental stages, a single pupa is the result of successful competition of one parasite larva that completed its develop-

ment and eliminated its competitors. Being a single one within a mummified aphid, it has no competitive possibilities either.

- SUPERPARASITISM. Superparasitism was commonly recognized in a number of parasite species both in laboratory and field conditions, by a number of authors, some of them being mentioned below:

In field samples, HAFEZ (1961) when dissecting several thousand *Brevicoryne brassicae* found, at the maximum, 13 first instar larvae of *Diaeretiella rapae* in one aphid. The undermentioned authors give the following numbers of parasite developmental stages to be found in a single aphid: SCHLINGER & HALL (1961)—maximally 10, often 2-3, for *Trioxys complanatus*. STARÝ (1963)—commonly 2-3, for *Aphidius ervi*, ARTHUR (1945)—sometimes 6-8, for *A. avenae*. BEIRNE (1942)—maximally 6, often 2-3, for *Praon volucre*, ULLYETT (1938)—1-8, for *Diaeretiella rapae*.

In the laboratory, superparasitism was caused either purposely or accidentally in the rearings. The following records may be mentioned: SCHLINGER & HALL (1960)—not common, for *Praon exoletum*. STARÝ (1964, 1966)—maximally 6, for *Aphidius megourae*. WIACKOWSKI (1962)—maximally 13, for *A. smithi*. FORCE & MESSENGER (1965)—maximally 31, for *Trioxys complanatus*.

SALT (1961) summarizing the knowledge on competition among insect parasites, recognized 4 basic types of competition among the solitary internal parasites: Deliberate physical attack, physiological suppression, accidental injury, and selective starvation. The first two kinds were mentioned as occurring in the aphid parasites.

In case of physical attack, the supernumerary larvae are eliminated by the surviving larvae through the use of mandibles. However, physical attack was mentioned as being used in first instar larva only, as this is the instar that exhibits large and strong mandibles in the Hymenoptera.

In case of physiological suppression, the supernumerary parasite larvae are killed by the surviving larva without any marks of violence on them. Various reasons, such as secretion, respiratory requirements, food, etc., were mentioned by various authors.

According to TREMBLAY (1966) we can divide all the opinions of various authors into three groups. It is necessary to add, that with respect to SALT (1961), the first group is identical with physical attack, while the second and third groups may be included under physiological mechanisms of SALT.

1. Mechanical, either purposely or accidental: ARTHUR (1945), BROUSSAL (1963), LOPEZ CRISTOBAL (1946), VÉVAI (1942), WEBSTER & PHILLIPS (1907, 1912), WHEELER, (1923).

2. Lack of oxygen and food: HARTLEY (1922), WIACKOWSKI (1962).

3. Enzymatic: JOHNSON (1959), MACKAUER (1959), MILLAN (1956), SPENCER (1926), TIMBERLAKE (1910).

Various other authors observed the occurrence of superparasitism under various conditions, but they either did not pay attention to its mechanism, or they explained it only generally, according to most opinions of various authors: ARTHUR (1945), BEIRNE (1942), FORCE & MESSENGER (1965), HAFEZ (1961), MACGILL (1923), SCHLINGER & HALL (1960, 1961), STARÝ (1964, 1966), SUBBA RAO & SITARMA (1962), ULLYETT (1938), etc. Generally, a somewhat detailed study on parasite bionomics includes also a short note on superparasitism.

The apparently most summarizing and widely experimentally founded paper has been published by TREMBLAY (1966), whose conclusions are mostly followed in this book.

First and higher instar parasite larvae exhibit somewhat different effects as to the competitive relations to other parasite developmental stages present in the aphid. In

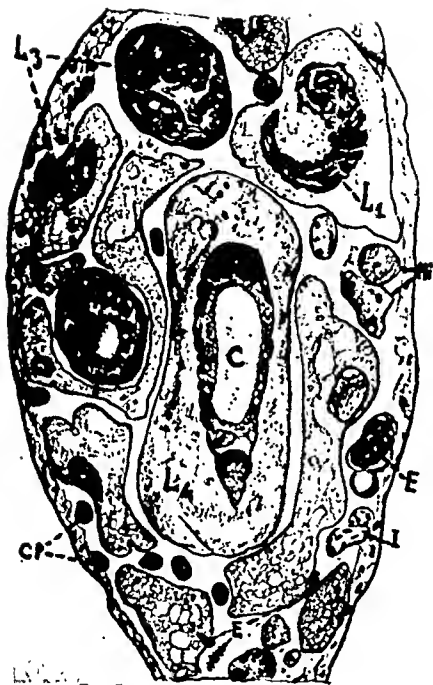


Fig. 263. A section through *Aphis fabae* (apterous virginoparous ♀) containing three larvae of *Lysiphlebus fabarum* (L₁, L₂, L₃) and various degenerating embryos of the same species in various stages (E). L₄ larva is hyperparasitized by a larva of *Charips* sp. (C). CP - pseudoserosal cells, I - rests of intestinal part of alimentary canal of the aphid, Mi-rests of aphid mycetozoa. The remaining part of the aphid body is occupied by enormous cells deriving from the embryonic envelopes of L₂ and L₄ (TREMBLAY, 1966).

the presence of a first instar parasite larva, the competing embryos whether just at the beginning of their division or in more advanced stages were constantly found in degeneration; the simultaneous degeneration of numerous young host embryos was also observed. In the presence of a mid-stage parasite larva, the coexisting parasite embryos showed a normal aspect when in their early embryogeny, while having a degenerative appearance when very advanced in development (Fig. 263). This type of coexistence was greatly influenced by the size of the host.

According to TREMBLAY (1966), the mechanism of competition among the various developmental stages of parasites inside an aphid is a combination of physiological and accidental mechanical injury.

The newly hatched larva diffuses into the host's haemolymph some cytologic secretion, which visibly affects the young host embryos and, concurrently, every competing embryo of the parasite itself. The secretion has no durable effect and the older parasite larvae show no capacity to induce the sudden degenerative changes attributable to the newly hatched ones; the elimination of the competing embryos, in the presence of a developed parasite larva, is achieved by subtraction of substances or elements essential to life (physiological suppression). Other conditions occur in which the elimination is achieved by accidental physical injury.

As to mechanical injury, we should like to add that several authors either found the mandibles of other instars in the guts of higher instar larvae (VEVAT, 1942, ARTHUR 1945), or they directly found a parasite larva with its mouthparts attached to another larva (FORCE & MESSENGER, 1965) or feeding on it (SCHLINGER & HALL, 1961). TREMBLAY's opinion (1966) is that parasite-host dimensional ratio has a decisive influence on the realization of the conditions determining the occurrence of physiological suppression or accidental injury.

There is a final effect of superparasitism as a competitive relationship among the parasite larvae of the same species within a single host aphid: Only a single parasite larva, the most powerful competitor, owing to various reasons, survives and successfully completes its development. This conclusion, irrespective of various opinions on the mechanisms of competition, has been uniformly supported by all authors.

- Factors. 1. Geographic distribution can restrict the host range of widely specialized species to a considerable degree in certain parts of their distribution area. This might also have an influence on the occurrence of superparasitism (see below).

2. Seasonal history. In certain periods of seasonal history of host and parasite the density ratio may change for the parasite, so that a higher degree of superparasitism can be observed. This seemingly is the period when the parasite population becomes high but has not yet dispersed to the neighbourhood.

3. Host range. Widely specialized parasites might seem to have a better chance of avoiding superparasitism than the strictly specialized species, as they can find other suitable hosts in the environment in case of a too low host population, which the specialized species cannot do. However, the observations of various authors show that this factor is overruled by the dispersal and other regulating factors (action of hyperparasites, etc.). Superparasitism was observed both in strictly specialized species (parasites of *Therioaphis trifolii* in California, see: SCHLINGER & HALL, 1960, 1961) and in widely specialized species (SKRIPTSHINSKY, 1930, STARÝ 1966, etc.).

4. Host species preference. The host species included in the host range of a parasite species differ from each other in a certain way. These differences may or may not change during the season.

One of such differences is the type of colony in which the aphids occur as well as the wax-cover, etc. For example, on Brassica crops, in a certain part of the season *Brevicoryne brassicae* colonies are rather dense and the aphids produce rather strong

wax covers. On the same plants, *Myzus persicae* occurs as well, whose colonies are more dispersed and they hardly produce any wax cover. Both species are parasitized by *Diaeretiella rapae*, however, apparent preference can be noticed and this could lead also to a stronger superparasitism in case of lower density of the preferred species.

5. Host instar preference. Parasite ♀♀ of various species are generally known to exhibit a host instar preference. Under certain conditions the preferred instar may be less numerous so that more ♀♀ are concentrated to those preferred instars, although the total density ratios may seem favourable. In consequence the instar preference may cause a higher degree of superparasitism.

6. Discrimination of parasitized and non-parasitized hosts. ♀♀ of some species do not distinguish living parasitized and non-parasitized aphids, which they themselves or other ♀♀ had already parasitized, for example, *Trioxys complanatus* (SCHLINGER & HALL, 1960). Other species exhibit a certain degree of discrimination ability. Numerous observations can be mentioned (see: Host specificity).

7. Density of populations. Relations in host-parasite population density are often the cause of superparasitism. Superparasitism is a feature of a case of too high a parasite density.

8. Searching ability is different in various species. Some parasite species are able to find hosts even in the case that they are very rare; other species are not. If the parasite density is favourable, high searching ability is useful to enable the parasite to find its host even at a very low density, although under high parasite density and low host density the high searching ability leads to a high degree of superparasitism. This phenomenon can well be observed in the laboratory rearings.

9. Oviposition behaviour of parasite female plays an important role in superparasitism, for example, in connection with host specificity features. Great differences can be found among the various species of parasites in this respect. Moreover, oviposition behaviour is deeply influenced by a number of various factors such as host suitability, the oviposition chances, etc. (see Oviposition).

The long absence of the host, i.e. a long period where there is no chance of ovipositing, is rather a strong stimulus to a parasite ♀. Later, when the host is present, the rather stimulated oviposition urge forces the ♀ to oviposit very rapidly so that often one and the same host specimen is attacked several times at very brief intervals. This phenomenon was observed by many authors and confirmed by our own observations.

The number of eggs laid during each insertion of the ovipositor is also important. Although usually a single egg is laid at each insertion, the depositing of no eggs being less common, there are cases known when the parasites laid two or several eggs during one insertion. SCHLINGER & HALL (1961) found as much as nine first instar larvae and one second instar larva of *Trioxys complanatus* after 76 hours, although the *Therioaphis trifolii* aphid was stung only once by the parasite.

10. Physical reaction of the host to parasite female attack. Some aphids exhibit no physical reactions as a response to parasite attack: in this case there is a greater possibility for such aphids to be superparasitized. Other aphids, on the contrary, exhibit strong adversary stimuli, they sometimes try to escape, etc., which sometimes can make a further oviposition impossible, preventing simultaneously superparasitism as well.

11. Reproductive capacity. Species with a high supply of eggs appear to manifest a greater degree of superparasitism under certain conditions than the species where the supply of eggs is low. This is, however, a factor that is rather influenced by other factors, such as oviposition behaviour, searching ability, density ratios, etc.

No. eggs per host	Number of hosts			
	P. palitans		T. utilis	
	21°C	27°C	21°C	27°C
0	7	24	9	4
1	8	22	20	21
2	15	14	16	16
3	19	13	11	16
4	15	12	11	12
5	14	5	7	8
6	8	6	5	7
7	6	1	5	5
8	5	3	4	3
9	2	0	3	4
10	0	0	2	2
11	0	0	2	1
12	1	0	2	0
13	0	0	1	0
14	0	0	0	1
>15	0	0	2	0

Table 11. Frequency and degree of superparasitism produced when three ♀ parasites attack hosts in small vials at two different constant temperatures. Data are proportions of 100 hosts parasitized with the indicated number of eggs. Parasites: *Praon exoletum* (= *palitans*), *Trioxys complanatus* (= *utilis*), (FORCE & MESSENGER, 1965).

12. Temperature was recognized to have a great influence on the degree of superparasitism. FORCE & MESSENGER (1965) showed that when three *Praon exoletum* ♀♀ were allowed to oviposit together for 24 hours in 50 hosts at 21°C they each laid the same average number of eggs as did a single ♀ ovipositing in the same number of hosts, as a great degree of superparasitism resulted from such crowding. Higher temperatures, which are less favourable for the parasite such as 27°C, caused less eggs to be laid per unit of time, but still a moderate amount of superparasitism occurred. Cooler environments reduced parasite motility and caused the ♀♀ to attack nearby hosts over and over again.

As the temperature requirements are specifically conditioned, the same temperature conditions influence the parasites and the degree of superparasitism in different ways. Experiments undertaken by FORCE & MESSENGER with *Praon exoletum* and *Trioxys complanatus* under 21°C and 27°C temperature conditions (Table 11) illustrate this influence.

13. Dispersal can also be classified as a prevention of superparasitism. Under natural conditions with the possibility of dispersal in case the density ratio is less favourable for the parasite superparasitism is generally rarely encountered. In the laboratory, on the contrary, where there can be unfavourable density ratios of host and parasite populations in a restricted space such as a rearing cage, superparasitism was observed by various authors to be rather common. Superparasitism, too, may best be obtained through intentionally produced unfavourable density ratio in a restricted space such as a vial or a Petri dish.

14. Hyperparasites and other natural enemies. The action of hyperparasites reduces the density of primary parasite population and causes simultaneously less probability of superparasitism through preventing the primary parasite population reaching overpopulation numbers.

15. Insecticides may influence host and parasite in various ways. Selective insecticides may substantially reduce the host population, while the parasite population is reduced to a much lower degree. In consequence, unnatural density ratio appears. Before such conditions are changed due to parasite dispersal, etc., superparasitism could be observed in a given treated plot. Although we have numerous observations of various authors on the effect of insecticides at hand (see: Integrated control), similar observations on superparasitism seem to be missing.

The factors mentioned above can be divided in two groups, extrinsic and intrinsic. The relations in and between both the groups are different, their prevalence being dependent on the given species.

An example illustrating such relations: climatic conditions of a given area influence the seasonal history of host and parasite species. Host and parasite density relations influence the degree of superparasitism. Temperature conditions, however, influence density ratios, oviposition behaviour of the parasite, its searching ability, host reactions, dispersal, etc.

— *Influence on the parasite.* A final result of superparasitism is that only a single larva survives and successfully completes its development. The survival of this single larva is possible by its successful competition with the other larvae that are supernumerary with respect to aphid-parasite relations. Therefore, the influence of the mentioned larva on the supernumerary larvae is lethal. However, superparasitism has also an influence on the surviving larva itself. According to observations of FORCE & MESSENGER (1965) the surviving larva of *Praon exoletum* was found to develop more slowly than larvae of the same age developing in non-superparasitized aphids. The authors consider this fact possibly because the supernumerary larvae during the time that they live within the host, usurp valuable nutrients, oxygen, or other physiological necessities from the eventual survivor.

— *Influence on the host.* For the time being, two influences are known of superparasitism with respect to the host:

SPENCER (1926) mentioned multiple oviposition as having no apparent effect on the superparasitized host except where the aphid has been oviposited many times, where a slight sluggishness is manifested.

JOHNSON (1959) observed superparasitism to exhibit, in some cases, a different influence on the host than in the case of single parasitism. Such differences were found in superparasitism of higher instar of apteriform versus alariform nymphs (*Aphis craccivora*—*Lysaphidius platensis*).

— *Significance.* Superparasitism may be classified from the two following points of view, with regard to the species itself, and with respect to the community.

In some species, superparasitism due to poor discrimination of parasitized and non-parasitized aphids seems to be a common intrinsic phenomenon. It occurs here without any pressure of the environment, consequently, it can be classified as a wastage of eggs. Nevertheless, this kind of wastage is not entirely complete, as superparasitism can also mean a greater probability of parasitization than a single parasitism. In single parasitism, as we have already mentioned, eggs may or may not be deposited during each insertion of the ovipositor, while a repeated insertion can mean either an egg to be really deposited, or superparasitism. While this function of superparasitism as an intrinsic phenomenon seems to be a relatively rare one, its main role, as an extrinsic phenomenon, seems apparently to be in reducing the parasite population density in case the host population is too low and the parasite density could increase with corresponding adverse later effects as to the survival of a parasite population in a given community. A third, and somewhat adverse effect of superparasitism seems to be in its mechanism, as the oldest larva present in the aphid is the

successful competitor, while at the same time, it need not be the best progeny.

As to the community, superparasitism may be important as one of the mechanisms regulating the parasite population density.

— BIOLOGICAL CONTROL. Superparasitism as a factor of specific value must be classified as an adverse character in parasite species biology, in introduced species namely, as it reduces the parasite effectiveness through the wastage of eggs.

Superparasitism caused by environmental factors must be classified with respect to these factors within the frame of the whole community studied.

Finally, laboratory rearings in a parasite introduction program must be organised in such a way as to avoid superparasitism as a factor reducing parasite effectiveness through purposely regulating density ratios, temperature, etc., in the rearings.

REFERENCES. 21-3, 65, 155-8, 290, 295, 314, 358-9, 419, 497, 510, 597, 672, 681, 685, 748, 754, 756, 762, 806, 960, 972, 1003, 1005, 1022, 1048, 1050, 1062, 1101, 1111, 1121, 1158, 1214, 1232-3, 1238, 1254, 1277, 1285, 1292, 1299.

Interspecific Relations

Aphids are a group of phytophagous insects that is rather numerous both as to the number of species and individuals. During its evolution it has inhabited the greatest part of habitats where plants can be found, although a certain differentiation may be recognized in this distribution favouring the temperate and subtropical zones. The occurrence of such a phytophagous group in various habitats has naturally been followed by the adaptation of various other groups such as natural enemies of aphids. Various insect groups have taken part in this action, the Hemiptera, Neuroptera, Diptera, Coleoptera, Hymenoptera, etc. These natural enemies must be considered, on the one hand, as beneficial agents with respect to a given community preventing outbreaks of phytophagous species, on the other hand, their action is useful for the aphids, as natural enemies prevent outbreaks that could result in a devastation of food sources (plants) and the elimination of an aphid population in a given community (see: POURT, 1960); finally, the relationship is favourable for the natural enemies too enabling their successful occurrence in various communities.

Although the original adaptation of various natural enemies to aphids, as their food, was apparently accidental and was caused by free ecological valencies in a community equilibrium, the long period of evolution has resulted in today's state, where various complexes of natural enemies may be recognized in different environments. These complexes include, besides other organisms such as fungi or birds, the insect predators and the parasites—the Aphelinidae, Mymaridae, and the Aphididae. As the primary natural enemies they themselves are also regulated in action through the action of their own parasites, various other groups being included in today's food chains as well, etc.

With respect to groups, we can consequently distinguish the relations among the primary parasites of the same or another group, between primary parasites and hyperparasites, between predators and parasites, between predators and their parasites, between natural enemies and fungi, etc.

All the cases above mentioned clearly show that there is a great possibility of various complicated relations arising. These complicated relations really can be found in nature, although being unsatisfactorily known in many cases. Moreover, they may not be related to a given aphid species only, as their host range enables them to stay as members of food chains associated with other aphids.

— KINDS OF INTERSPECIFIC RELATIONS. We recognize two different points of view on interspecific relations mentioned in the literature.

— Competition concept — Most authors usually classified any relations among the parasites or other natural enemy species as a competition. This seems to be a result of a general acceptance of 'struggle of species' as mentioned by DARWIN. For example, ULLYETT (1938) excellently classified the aphid and natural enemy food chains with respect to separate groups; however, hyperparasitism and competition were the only relations mentioned as occurring among the parasites. SCHLINGER & HALL (1960), when dealing with the aphidiids of California, mentioned *Diaeretiella rapae*, besides its parasitism on *Brevicoryne brassicae*, to be one of the species most often seen attacking *Myzus persicae* and frequently occurring in direct competition with *Ephedrus persicae*, *Lysiphlebus testaceipes*, and *Aphelinus* spp.

A similar viewpoint is mostly accepted when an introduced species is classified with respect to indigenous parasites in the country of parasite establishment. There, too, the primary aspect is the competition with indigenous parasites. Many such examples can be mentioned. SCHLINGER & HALL (1960) classified the relations of natural enemy groups with respect to *Praon exoletum* introduction and its effectiveness in California. HAGEN & SCHLINGER (1960) dealt with the introduced parasite, *Aphidius smithi*, and indigenous parasites of *Acyrtosiphon pisum* in California. As to the 5 indigenous parasites established, they have considered their occurrence to be rare, and one of them (*Aphidius pisivorus*) to be incapable of competing with *A. smithi* in the laboratory, and in the field owing to its scarcity too. FORCE & MESSENGER (1964, 1965) in a very valuable paper on the relations of parasites of *Therioaphis trifolii* in the laboratory with respect to the field occurrence in California have used the competitive relations as the base for their studies. V.D. BOSCH, SCHLINGER & HAGEN (1962), dealing with *Chromaphis juglandicola* and its introduced parasite, *Trioxys pallidus* in California, considered the interspecific competition to be probably of little significance with respect to the indigenous parasites that were found to attack the introduced pest.

An example of an almost extreme application of a point of view of competition is that in the case of MACKAUER & BISHOP (1965). These authors classified the effectiveness of indigenous parasites of *Acyrtosiphon pisum* with respect to the introduced species, *Aphidius smithi*, in Canada. From the whole paper, which includes even a table as an illustration it is apparent that the indigenous parasites of the aphid mentioned are relatively rare in Canada, if we compare the occurrence of parasites in for example C. Europe. Of the parasites mentioned (*Praon pequodorum*, *Aphidius pulcher*, and *Praon* sp.), *A. pulcher* is just a rare species. Nevertheless, although it is apparent from the table that *A. pulcher* was not present at all in various fields studied, *A. smithi* is mentioned to be the dominant species, probably largely replacing the native *A. pulcher*, while *Praon pequodorum* seemed to be less affected by *A. smithi*. In our opinion, this is not a displacement but merely a situation showing that *A. pulcher* was rare and the introduced *A. smithi* had become more common. In several fields the populations of *A. pulcher* were lacking altogether, the introduced parasite having no possibility of displacing this species in consequence; or, the introduced species too was absent (Table 12). As the introduced species was unable to displace the common *Praon pequodorum*, it is hardly believable that it would do so in case of a rare indigenous species as the mechanism of competition apparently excludes such a possibility—*Aphidius smithi* would need to select just the aphids that were parasitized by *A. pulcher*, or to be so numerous that *A. pulcher* would be unable to find any healthy aphids; as to the former case, such a kind of competition would not favour *A. smithi* as *A. pulcher* would be—being an older one as to the date of para-

Location	Aphid Host Plant	Parasite Records			
		A. smithi	A. pulcher	P. pequodorum	Praon sp.
Co. Welland					
Chippawa	M. sativa	+	+	m	
Crystal Beach	M. sativa	+		m	
6. mi. E. Fort Erie	M. sativa	+		+	
Co. Lincoln					
Queenston, Hwy. 8 at Davids R.	M. sativa	+		x	+
Queenston, Hwy. 8 at Martin R.	M. sativa	+		+	
St. Catharines, Airport	M. sativa	+		+	
Vineland, 7 & 17 St. Louth	M. sativa	x		+	+
Vineland, 7 & 19. St. Louth	M. sativa	x		m	
Vineland, 7 & 21 St. Louth	M. sativa	x		+	
Co. Halton					
5 mi. W. Palermo	M. sativa				+
Campbelville	Vicia sp. Melil. alba			m	
Co. Peel					
Brampton	M. sativa	+	+		
Co. Prince Edward					
Consecon	M. sativa	+	+	x	+
Co. Hastings					
Frankford	M. sativa			+	+

Table 12. Records of *Aphidius smithi* in southern Ontario (1964). Symbols: (+) Collecting and rearing record. (x) Most abundant species in sample taken. (m) Mummies collected but no adults emerged; identification to species not possible at present. (MACKAUER & BISDEE, 1965).

sitization—the successful survivor; as to the latter case, the introduced parasite was not so common.

Competitive relations (see below) also became the subject of great discussion with respect to the number of parasite species to be introduced.

— Cooperation concept — Detailed analysis of the structure of communities and natural enemy (parasite) action has shown that relations among the natural enemies are more complicated. Competitive relationship, naturally, occurs, but this is only one kind of the relations possible. FRANZ (1961, 1964) has summarized the kinds of relations among the natural enemies, and recognized three kinds or degrees, i.e. cooperation, competition, and displacement, respectively. Consequently, enemy action as a whole results from the complementary total sum of a single species action differing in many ways (FRANZ, 1964). We have only to strongly support this concept with respect to aphid parasites as members of aphids-natural enemies food chains. According to our opinion, there is a state of relative unity among all three kinds, they condition each other: under the influence of environmental factors,

cooperation may condition competition and displacement; similarly, the displacement may result in further cooperation, with respect either to the same or other species, etc.

– *Cooperation.* The evolution of parasite complexes is a sign of cooperation. As mentioned above, there may be various enemy complexes differentiated among the natural enemies of aphids. However, because of a different evolution of all these groups together with the evolution of aphids, the role of different groups in attacking different aphid groups is different. All the groups of natural enemies, and all their members were studied in detail, exhibit an apparent relation with respect to their aphid hosts. Although some groups seem to be widely specialized, a closer analysis shows that there is a host range in all the groups. The restricted host of separate groups or species results in that they do not attack certain aphid groups, but such aphid groups are attacked by other natural enemy groups so that apparently no aphid group free from natural enemies can be found. The ability of natural enemies to develop such complexes that are independent as to taxonomic affinities, but which are closely related in action, seems to be a result of evolution with a trend to cooperation.

The forementioned can well be illustrated by the aphidiid wasps. There are certain aphid groups such as Adelgoid aphids that are not attacked by the aphidiids at all. This is apparently due to the phylogeny of the parasite group, which has become adapted to the ancestors of the recent Aphidoid aphids during the period when the two main aphid groups were differentiated. The lack of aphidiids as parasites as enemies of Adelgoid aphids, however, does not mean that this group is free of enemies—various other natural enemy groups covered these aphids under their host range. This is perhaps the result of cooperation in evolution. The same trend may often be found inside the aphidiid parasites as a group, being apparent from the geographic distribution of the parasites, habitat distribution, and microhabitat distribution as well as from other features of their biology. In addition, we should mention that both parasites and predators as members of aphids-natural enemies food chain exhibit both positive and negative features. This is obvious from the fact that in most of aphid-natural enemies food chains both predatory and parasitic organisms are represented, although great differences in their relative representation may occur.

Complementary action of parasites (and other natural enemies) in time and space is another sign of cooperation. A research of natural enemies of a given aphid species undertaken in a given country shows gradually a great number of various species taking part, however, simultaneously, these species are very rarely or almost never found to be represented in a single sample. Various factors play a part here, but generally this is a result of complementary action in time: In case that a given natural enemy species is lacking, the other species replace it. Many examples from our field observations might be mentioned, the most numerous and most obvious due to their quantity are those connected with the research of natural enemies of *Aphis fabae* in Czechoslovakia (HODEK et al., 1966):

There is a spacious park in Prague, an example of an old biocenosis. Observations of the occurrence of natural enemies of *Aphis fabae* in different years resulted as follows:

22.5.57: *Anthocoris nemorum*, *Adalia bipunctata*, *Ephedrus plagiator*, *Praon abjectum*, *Trioxys angelicae*

2.6.57: *Anthocoris nemorum*, *Praon abjectum*, *Trioxys angelicae*

8.5.58: *Ephedrus plagiator*, *Trioxys angelicae*

- 1.6.58: *Anthocoris nemorum*, *Epistrophe balteata*, *Ephedrus plagiator*, *Praon abjectum*,
Trioxys angelicae
 24.5.59: *Trioxys angelicae*
 21.6.59: *Trioxys angelicae*

The occurrence of natural enemies of *Aphis fabae* was also found to be different on different shrubs of *Euonymus europaea* in the same locality, or to be rather similar in very different localities:

Moravia, Pohorelice (hedges):

- 19.5.60 (shrub A): *Adalia bipunctata* L., *Trioxys angelicae*
 19.5.60 (shrub B): *Semiadalia undecimnotata* SCHNEID., *Praon abjectum*
 19.5.60 (shrub C): *Syrphus vitripennis* MEIG., *Cantharis rustica* L., *C. fusca* L., *Ephedrus plagiator*, *Trioxys angelicae*

A similar situation was found on secondary host plants of *Aphis fabae*:

Raná Bohemia, (sugar beet field)

- 26.5.59: *Semiadalia undecimnotata* SCHNEID., *Coccinella septempunctata* L., *C. quinquepunctata* L., *Adonia variegata* GOEZE
 16.6.59: *Semiadalia undecimnotata* SCHNEID., *Coccinella septempunctata* L., *C. quinquepunctata* L., *Scaeva pyrastris* (L.), *Syrphus ribesii* (L.).

From other fields of the same locality there are the following results:

- 18.6.57 (field A): *Lysiphlebus fabarum*
 18.6.57 (field B): *Semiadalia undecimnotata* SCHNEID., *Lysiphlebus fabarum*
 18.6.57: *Adonia variegata* GOEZE
 26.5.59: —
 19.6.59: —
 26.6.59: *Scaeva pyrastris* (L.), *Syrphus ribesii* (L.)
 17.6.59: *Coccinella quinquepunctata* L., *C. septempunctata* L.

The last illustrative example is from Central Bohemia (Polabí): Český Brod (sugar beet fields):

- 28.7.60: *Chrysopa carnea* STEPH., *Epistrophe balteata* (DEG.), *Sphaerophoria scripta* (L.), *S. rueppellii* WIEG., *Syrphus ribesii* (L.), *S. vitripennis* MEIG., *Coccinella quinquepunctata* (L.), *C. septempunctata* L., *Adonia variegata* GOEZE, *Semiadalia undecimnotata* SCHNEID., *Propylaea quatuordecimpunctata* (L.), *Lysiphlebus fabarum*.

Other numerous examples can be found in the book by HODEK et al. (1966).

Another feature is natural enemy cooperation in space: *Aphis* specimens which are not found by one natural enemy species will be detected by another (see: FRANZ, 1964). Many examples can be mentioned here. Microhabitat distribution as well as the searching capacity of parasites cause that a single aphid species can be attacked by different parasite species in dependence whether occurring on the tops of plants or underneath the leaves. Similarly, small aphid colonies sometimes seem to be found and attacked earlier by coccinellid beetles than by the parasites, e.g. in the annual crops, where the searching behaviour as well as natural enemy dispersal play their role.

— *Competition*. 1. Ecological groups of parasites and interspecific competition. Gregarious parasite species do not fight for possession of the host for the fighting as a means of elimination of a competitor is incompatible with the gregarious habit. It is concordant with this that supernumerary larvae of gregarious parasites (parasitoids) are not necessarily eliminated at an early stage, as they are among a solitary species, but often persist until they are nearly fully grown (SALT, 1961). Gregarious internal parasites can be found neither among the primary parasites of aphids, nor among the hyperparasites.

Among the external parasites, as among internal parasites, fighting between com-

petitors takes place in the solitary species, but is not found in the gregarious species (SALT, 1961). Such relations can be found among certain hyperparasites of aphids, which are solitary external parasites of the aphidiid wasps, or their solitary internal hyperparasites.

Several solitary internal parasites can sometimes be found in a single host. Consequently, supernumerary larvae are eliminated as only a single larva completes its development. This is the case of primary parasites of aphids, the aphidiids as well as other groups of primary parasites of aphids.

2. Interspecific competition among various developmental stages. Interspecific competition among parasite adults can be recognized by their searching ability, oviposition behaviour, host instar preference, discrimination between parasitized and non-parasitized aphids, seasonal occurrence, dispersal, fecundity, progeny, etc. These features are mentioned below in detail.

The laid eggs do not seem to reveal competitive action similarly as in the case of superparasitism.

The larval stage is just the stage where intensive competition among the parasite species can be seen. This competition for food sources is caused by the deposition of eggs of several parasite species in a single host (multiparasitism). Both morphological and physiological features of the larvae apparently give the best possibility for direct competitive relations when the developmental stages are compared.

A single larva, either developed freely from a single egg, or being a survivor in competition with the larvae developed from several eggs laid, develops and pupates inside or under the parasitized aphid. Consequently, there cannot be direct competition among the pupae. However, the mode of pupation is different in certain parasite groups, and it seems to have a certain significance with respect to survival of unfavourable conditions in a similar way as the development of quiescent and non-quiescent cocoons.

SMITH (1929) recognized two kinds of competition with respect to parasite stages: (1) Intrinsic competition—competition between parasitic larvae within the body of the host, (2) Extrinsic competition—environmental relationships of the adult parasites outside the host, such as fighting among adults, differential survival to physical factors, etc.

3. Multiparasitism. Various authors mentioned in a more or less detailed way certain notes on interspecific relations among the parasites. However, most of them include field observations as to different seasonal occurrence, microhabitat occurrence, etc. (HASSAN, 1957, SKRIPCHINSKIY, 1930, TELENGA 1950, V.D. BOSCH et al., 1964, etc.). Records dealing directly with multiparasitism are relatively rare. HARTLEY (1922) was perhaps the first who studied a direct case of multiparasitism, that of *Aphelinus semiflavus* and *Aphidius*-species. A similar case was studied by GRISWOLD (1927). The mechanism of competition in aphids parasitized by *Aphidius*- and *Aphelinus*-species was undertaken by FORCE & MESSENGER (1965), based on field observations of various authors (see: V.D. BOSCH et al., 1964) and planned as a further base for the research of competitive relations among the parasites in the field.

The research of mechanisms of competition among parasite larvae of different species generally reveals the same features as in a case of superparasitism, although the number of papers dealing with multiparasitism is smaller (HARTLEY, 1922, SPENCER, 1926). Apparently, the mechanism of competition among the parasite larvae will be of the same kind as in a case of superparasitism (see: TREMBLAY, 1966), i.e. combination of physiological suppression and accidental physical injury seem to come into action.

The final effect of multiparasitism in aphid parasites, either among different species

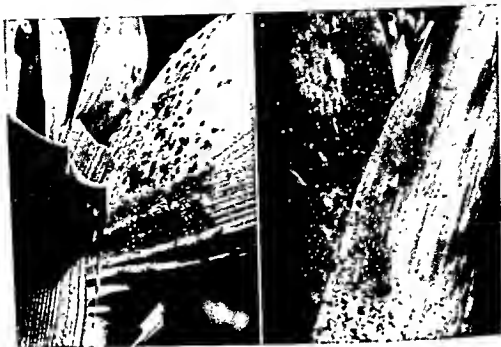


Fig. 264. Right: *Rhopalosiphum maidis* on *Zea mays* parasitized by *Lysiphlebus testaceipes*. Left: the same aphid parasitized by an *Aphelinus*-species. Cuba.

of aphidiid wasps or any aphidiid wasps and other groups of primary parasites of aphids, is that a single larva survives which eliminated all the supernumerary larvae during its development in a single host.

Therefore, with respect to FISKE's (1910) classification of multiparasitism, multiparasitism in aphid parasites seems to be favourable that due to a limited food-supply—a single aphid specimen—all the supernumerary larvae are eliminated, although a single larva survives and successfully completes its development.

4. Relative meaning of the avoidance of interspecific competition. SALT (1961) divided the parasites into two groups with respect to competition, i.e. species avoiding and not avoiding competition. In our opinion, whether such an avoidance is via selection and differentiation of parasitized hosts, etc., this does not mean an avoidance of competition, as by avoiding competition of its larvae in a host, such a parasite may be successfully adapted as to the competition with other species. Therefore, such an avoidance of competition is only relative. Observations of FORCE & MESSENGER (1965) made on parasites of *Therioaphis trifolii* can be mentioned as an example: There, *Aphelinus semiflavus* was found to be favourable in discriminating to a high degree of parasitized and non-parasitized aphids, tending to avoid wastage of eggs through superparasitism and mostly through multiparasitism too; naturally, other features of parasite biology can substantially reduce this advantage, such as slow searching behaviour and oviposition, etc.

— Displacement. The period and degree of parasite adaptation to environmental conditions such as climate, microclimate, host life-cycle peculiarities, etc., all these have played a role during the evolution of the parasites. The main developmental trend, i.e. to cover the host organisms in all the environments may well be recognized in the parasite group as well. Naturally, certain favourable conditions were found to be suitable by a single or different species. Consequently, competitive pressure

originated and the best adapted species became the most successful, while the other species were forced to cover new environments—for example, other niches, periods of the season, etc. Such a pressure occurred either in case of free niches, or in case that a better adapted species developed such a pressure on an older species resulting in displacement. Consequently some species favoured finding new niches, others were forced to do so, and some were eliminated due to lack of adaptation. In aphid parasites, the total displacement of a species by another species seems to be rare. Mostly, a better adaptation of a species for a given niche, etc., appears, resulting in further differentiation of species as to the niches.

Displacement of species is a long process. Sometimes we observe it to be a brief one owing to the action of man, in cases of eradication of certain pests and their replacement by other (insect) species. Some cases of specific displacement are known in the praxis of biological control as well.

— **RELATIVE STABILITY.** Interspecific relations are a result of a long evolution of various organisms under various environmental conditions. This means that the stability of such relations is relative in a similar way as that of the environment. The influence of some environmental conditions is rather long: For example, virgin forest natural communities have developed for a very long period, the relations occurring there are relatively stable. True forest aphid groups are rather old groups as to the phylogeny of the whole aphid group, and they exhibit rather specialized parasite fauna. A similar stability seems to occur in the interspecific relations that take place in such closed communities. Similar conditions can be found in a virgin steppe. All these relations are influenced primarily climatically through the occurrence of plant communities, and the aphid and parasite occurrence too, which followed. However, man's activity resulted in the creation of a number of new environments, which are man-modified and may not be found in natural environments. Consequently, new interspecific relations originated: some of the natural relations remained unchanged, others changed and some were eliminated. Classical examples can be seen in the case of cultivation of virgin steppe undertaken in various communities (U.S.S.R.). Parasites, as members of the food chains, are influenced by man's activities to various degrees as well. New conditions for aphid life caused new enemies in the natural enemy group: We can cite the differences in the natural enemy dispersal in virgin and cultivated lands.

Irrespective of the stability of a given community, interspecific relations can change during a season within the frame of a given community: Various parasites (and natural enemies) occur in different parts of the season and consequently fall under different relations. Another example can be found with respect to the response of natural enemies to obligatory host alternation of aphids in the temperate zone: some predators may follow the aphids and consequently occur in habitats of different kinds; the parasites, on the contrary, have developed another adaptation; as a result, there appear different interspecific relations among the natural enemies in the course of the season.

— **FACTORS.** This is a short review of factors that may be important with respect to interspecific relations of parasites. More detailed information can be obtained in corresponding chapters. Some examples are added to illustrate the influence of different factors.

1. Duration of developmental period and generation time. Under the same conditions the length of the developmental period may distinguish the species and also influence the generation time. It is apparent that a species with the shortest developmental period is also able to parasitize the hosts at a time when the other species are still unable to do so, being in larval or pupal stages. Consequently, such a species may

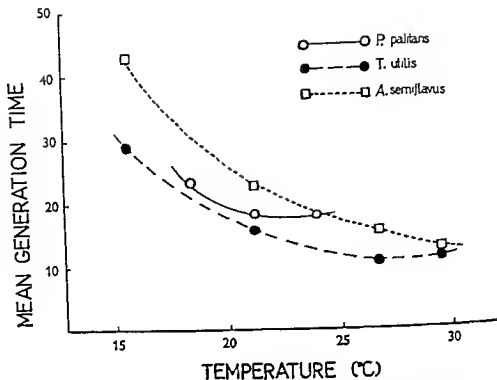


Fig. 265. Comparison of the mean generation time, calculated from the relation $T = \log_e R_e / r_m$ of 3 parasites of *Therioaphis trifolii* (= *maculata*), reared at several constant temperatures. Means are based on 10 replicates (FORCE & MESSENGER, 1964).

be successful in competition (multiparasitism) as its larvae develop earlier inside parasitized aphids.

FORCE & MESSENGER (1964) dealt with three parasites of *Therioaphis trifolii* which were purposely introduced into California. Under various combinations of temperature and R.H. it was recognized that *Trioxys complanatus* had the shortest developmental period and generation time at the temperature tested; *Aphelinus semiflavus* had the longest generation time, its developmental period being the longest of the 3 species at intermediate temperatures, but was shorter than that of *Praon exoletum* at low and high temperatures; *Pr. exoletum* was intermediate between the other two parasites (Fig. 265-267).

2. Mode of pupation. There are two groups recognizable among aphid parasites: the first group includes species that pupate within the parasitized aphid, the other group spins its cocoon under the parasitized aphid and places the aphid skin on the top. Although there is no experimental proof, it seems that the pupation within a mummified aphid protects the pupa better against various injuries than the separate cocoon. We consider it to be so because the first mode is prevalent among the aphidids as a group, while the second one may be found to a smaller degree. Certain secondary adaptations in spinning peculiar quiescent cocoons were also recognized among the parasites.

3. Adult longevity is important in enabling a parasite species to find more hosts and to disperse in a higher degree in the environment. Significant differences in longevity were recognized by FORCE & MESSENGER (1964) in parasites of *Therioaphis trifolii* in California: (Figs. 265-267).

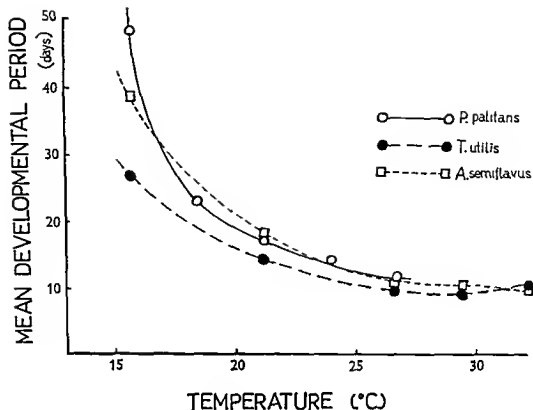


Fig. 266. Comparison of the mean developmental periods, from egg to emergence from the cocoon, of 3 parasites of *Therioaphis trifolii* (= *maculata*), reared at several constant temperatures. Calculated means are based on from 60 to several hundred replicates. Parasites: *Praon exoletum* (= *palitans*), *Trioxys complanatus* (= *utilis*), *Aphelinus semiflavus*, (FORCE & MESSENGER, 1964).

4. Reproductive capacity. The supply of eggs is different in various species. Although a number of factors cause the potential number of eggs not to be deposited, the relative number of eggs is important in interspecific relations. FORCE & MESSENGER (1965) found that of the three parasites of *Therioaphis trifolii* the total fecundity of *Aphelinus semiflavus* at 21°C was the highest and it oviposited at the lowest rate during the first three days of adult life; *Trioxys complanatus*, which nearly reached its total fecundity, exhibited the highest daily oviposition rate. At a higher thermal level, 27°C, *Aphelinus semiflavus* was stimulated to lay eggs at a somewhat higher rate, *Trioxys complanatus* was affected only slightly, and *Praon exoletum* was definitely adversely affected, ovipositing at a very decreased frequency early in life (Table 13).

5. Progeny. Parasite species that attack the same host species may differ in the mode of reproduction. Most of the aphidid parasites are biparental, while deuterotoky and thelytoky is rare. Uniparental reproduction seems to be more advantageous as the parasite ♀♀ can lay eggs without being mated, ♀ progeny, however, arising from such eggs, contrary to biparental species where unmated ♀♀ produce ♂ progeny exclusively and this may mean the elimination of a parasite population in a given plot. The mode of reproduction seems to vary in different strains of aphidid parasites, as the same species are known to be biparental in one part and uniparental in another part of their distribution area. In C. Europe, *Lysiphlebus ambiguus* is a biparental species, *L. fabarum* is a deuterotokous species. They also both differ with

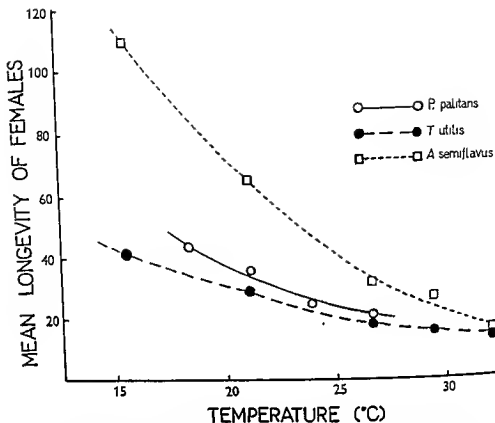


Fig. 267. Comparison of the mean ♀ life spans from egg to adult death of 3 parasites of *Therioaphis trifolii* (= *maculata*), reared at several constant temperatures. Means are based on 10 replicates (FORCE & MESSENGER, 1964).

respect to habitat preferences, the first one being attached to forest and the latter to steppe type habitats. However, they were found to occur in the same type of habitat as uniparental species, although being distributed with respect to different requirements on microhabitats, in Israel (ROSEN, 1967).

In parasites of *Therioaphis trifolii* in California, FORCE & MESSENGER (1965) found that *Trioxys complanatus* and *Praon exoletum* were biparental, these features being mentioned as resulting possibly in the extinction of local populations due to low population density and lack of contact between the sexes; contrary to the aphidiids, *Aphelinus semiflavus* was mostly uniparental, with no danger of extinction (Table 13).

6. Oviposition seems to be important with respect to oviposition rate and egg dispersal, and it is influenced by temperature, oviposition chances, etc. The parasites exhibit great differences in oviposition. Some species oviposit rapidly and frequently, the other species are slow or rarely ovipositing. Egg dispersal is also different.

Oviposition was found different in parasites of *Therioaphis trifolii* as well according to FORCE & MESSENGER (1965). *Trioxys complanatus* was very rapid and frequent in oviposition, *Praon exoletum* was less efficient, and *Aphelinus semiflavus* was inferior to the aphidiids in its slowness (Table 13).

Species	Total fecundity		Mean daily oviposition rate first 3 days		Innate capacity for increase	
	21°C	27°C	21°C	27°C	21°C	27°C
<i>P. palitans</i>	579	76	63	8	0.24	neg.
<i>T. utilis</i>	845	493	123	106	0.38	0.48
<i>A. semiflavus</i>	879	385	19	23	0.24	0.34

Table 13. Total fecundities, daily rates of oviposition during the first three days of adult life, and innate capacities for numerical increase of three parasites of *Therioaphis trifolii*.

Praon exoletum (= *palitans*), *Trioxys complanatus* (= *utilis*), *Aphelinus semiflavus* (FORCE & MESSENGER, 1965).

7. Searching ability. Higher searching ability of a parasite species may mean a higher number of parasitized hosts. Searching ability is most significant when host population is rather low. Low searching ability in these cases may mean a reduction of parasite population in a given plot.

Apparent differences in searching ability were found in parasites of *Therioaphis trifolii* under constant temperature conditions (FORCE & MESSENGER, 1965). *Trioxys complanatus* was very rapid in finding the host, *Praon exoletum* less efficient in its searching ability, while *Aphelinus semiflavus* was very slow.

8. Discrimination of parasitized and non-parasitized hosts is rather important in preventing wastage of eggs through superparasitism and multiparasitism.

In the parasites of *Therioaphis trifolii* (FORCE & MESSENGER, 1965) *Trioxys complanatus* and *Praon exoletum* were unable to discriminate between parasitized and non-parasitized hosts, which resulted in a higher degree of super- and multiparasitism under certain conditions; on the contrary, *Aphelinus semiflavus* was recognized to discriminate to a high degree between parasitized and non-parasitized hosts and thus tended to avoid wastage of eggs.

9. Host range, host availability. Generally, it seems that more widely specialized parasites have an advantage in interspecific relations as they can find their other hosts in the environment in case of lack of a given host, too severe interspecific competition, etc., while this is not the case of a strictly specialized parasite species. However, a strict specificity of a parasite is the result of long host-parasite relations, and consequently the adaptation of parasite to host occurrence, seasonal history, etc., seems to be far better than that in a widely specialized parasite. Another aspect of a wide host range is that the more species are attacked, the more interspecific relations may be simultaneously recognized. Nevertheless, it seems that a wider host range has apparently some advantage, as the strictly specialized parasite species are relatively very rare among the aphidids.

For example, there are two parasites of *Phyllaphis fagi* on *Fagus sylvatica* in C. Europe. *Trioxys phyllaphidis* is a strictly specialized species, while *Praon flavinode* is a parasite of a number of arboricolous Callaphidid aphids (STARÝ, 1966).

Dactynotus-, *Macrosiphoniella*- and related genera and their parasites can be mentioned as another illustrative example (STARÝ, 1966): among these parasites, *Trioxys pamonicus* attacking *Titanosiphon artemisiae* and *Aphidius phalangomyzi* parasitizing *Phalangomyzus oblongus* are the two strictly specialized parasites; the other parasites may either attack various species both of *Dactynotus*- and *Macrosiphoniella* species

(*Ephedrus campestris*, *Trioxys centaureae*), or they are further specialized to parasitization of *Dactynotus*- (*Aphidius funebris*, *Praon dorsale*) or *Macrosiphoniella* species (*Aphidius absinthii*, *Praon absinthii*): they, however, rarely attack the hosts of the above mentioned specialized parasites.

Host range can be influenced by host availability, which can be temporary due to peculiarities of the community, or perpetual due to different distribution of host and parasite. Under certain conditions, many specialized hosts may occur as strictly specialized species due to the lack of their alternative hosts in the environment. For example, *Trioxys pallidus*, an introduced species in California, was primarily able to attack the *Chronaphis juglandicola* aphid in the country of establishment, although it attacks a number of various arboricolous Callaphidid aphids in its native country, but these species do not occur in the country of establishment.

10. Host species preference. It is well known that certain species included in a host specificity range of a given parasite are preferred. Consequently, some adapted populations or strains may occur. The preference may result in various interspecific relations due to other members of parasite complexes. For example, according to SCHLINGER & HALL (1960) *Aphidius pisivorus* is most common as a parasite of *Acyrtosiphon pisum*, *Lysiphlebus testaceipes* not attacking this aphid in California. However, in New Jersey, *L. testaceipes* is an important parasite of this aphid, *A. pisivorus* not attacking the aphid there. Similarly, SCHLINGER & HALL (1960) found that *Diaeretiella rapae* is the main parasite of *Brevicoryne brassicae* in California; however, simultaneously, it attacks also *Myzus persicae*, where it comes into contact with other parasites such as *Ephedrus persicae*, *Lysiphlebus testaceipes*, and *Aphelinus* sp. Another example was found by us in a greenhouse in Czechoslovakia: *Neomyzus circumflexus* was highly infested by an *Aphelinus* sp., while this aphid was very rarely parasitized by *Diaeretiella rapae*; on the contrary, *Myzus persicae* was commonly parasitized by *D. rapae*, but it was very rarely found to be parasitized by the *Aphelinus* sp. Further, *Lysiphlebus fabarum* and *L. ambiguus* are well differentiated in C. Europe both as to host species preference and habitat occurrence (STARÝ, 1966), however, according to ROSEN (1967) they commonly attack *Toxoptera aurantii* on Citrus in Israel in similar kinds of habitats, while the aphid is absent in C. Europe.

11. Host instar preference. An evident host instar preference developed among the aphidids. Various studies have shown that species attacking younger instar aphids are more successful in cases of multiparasitism, as the elder parasite larvae survive in all cases. According to HARTLEY (1922) in competitive relations between *Aphidius* and *Aphelinus* species, *Aphidius* was more successful in attacking lower host instars. FORCE & MESSENGER (1965) found that among the three parasites of *Therioaphis trifolii*, *Trioxys complanatus* and *Aphelinus semiflavus* preferred younger host instars for oviposition, while *Praon exoletum* attacked higher host instars.

12. Seasonal occurrence. Seasonal history displays various peculiarities in separate species. Some of them occur earlier in the season due to their ability to survive lower temperatures in spring (temperature zone), etc. Features of seasonal occurrence can result in different interspecific relations occurring during the season. For example, different seasonal occurrence was found among the parasites of *Rhopalosiphum maidis* in Egypt (HASSAN, 1958). TELENKA (1950) observed *Aphis fabae*, *A. craccivora*, and *Brachycaudus cardui* to be parasitized by *Lysiphlebus fabarum* and *Aphelinus* sp. in the Caucasus; of these, *L. fabarum* was dominant in spring and autumn, while *Aphelinus* sp. was most common during summer. Such a seasonal difference was later shown experimentally to be due to different requirements in temperature conditions. Differences in seasonal occurrence were also ascertained in parasites of *Therioaphis trifolii* in California v.d. (BOSCH, 1964): *Trioxys complanatus* exhibited in most areas

intensive activity in early spring, depending on the area (x quiescent states). this activity may continue through spring and summer and on into the autumn, and even in winter. *Praon exoletum* is active principally in spring and late summer and autumn, but at best it is very feebly active in winter because of its quiescent state. *Aphelinus semiflavus*, in certain areas, reaches its most important status during winter, suffering greatly from the heat during summer.

13. Quiescent states in parasites developed as a response to unfavourable conditions of environment, either due to climatic conditions or host absence. For example, according to v.d. BOSCH et al. (1964) quiescent states may be found in a different degree among the parasites of *Therioaphis trifolii* in California; in *Trioxys complanatus*, quiescent states are found both to survive a hot summer period and sometimes unfavourable winter conditions as well. *Praon exoletum* exhibits quiescent states in a winter period only, while there is a lack of quiescent states in *Aphelinus semiflavus*. These differences considerably influence the occurrence of species and their relations in different areas. According to our observations, *Ephedrus persicae*, *E. plagiator*, and *E. cerasicola* are the common parasites of *Myzus cerasi* on *Prunus avium* in spring in C. Europe; however, *E. persicae* exhibits a quiescent state from late spring for the rest of the year, there being in consequence different interspecific relations among the parasites during the season.

14. Dispersal. The mode and kind of dispersal can be various in parasites and can have an influence on the interspecific relations as well. The species which attack higher instar aphids seem to exhibit better dispersal as their larvae disperse via parasitized alate aphids. On the contrary, a parasite species which attacks lower instar aphids, seems to be less dispersive in this respect. For example, among the parasites of *Therioaphis trifolii* in California (v.d. BOSCH et al., 1964), *Praon exoletum* prefers higher instar aphids and consequently its dispersal is more rapid than in the other parasites.

15. Temperature. In many respects, temperature has a major role, determining also the influence of other factors. FORCE & MESSENGER (1965) clearly showed the influence of temperature on interspecific relations among three parasite species of *Therioaphis trifolii* (Figs. 265-267, Table 13).

16. Superparasitism and multiparasitism. With respect to interspecific relations, both these phenomena can be classified as a wastage of eggs, as only a single larva completes its development in super- and multiparasitized hosts. Although being due to the influence of a great number of factors, the inability of a parasite ♀ to distinguish parasitized and non-parasitized hosts seems to play a major role. Among the parasites of *Therioaphis trifolii* super- and multiparasitism were found to be common in the laboratory (FORCE & MESSENGER, 1965); however, only *Trioxys complanatus* and *Praon exoletum* did not discriminate parasitized and non-parasitized hosts, while *Aphelinus semiflavus* avoided superparasitism and mostly multiparasitism by distinguishing the hosts.

17. Rarity of occurrence. Some parasite species are found to be common in nature, while others are less common to rare. Although the host specificity range, host preference, season, distribution, etc. play a role, there is no doubt about such a state. Species that are generally rare will apparently exhibit less interspecific relations than the commonly occurring species.

18. The foci of parasites can be very different in various ways as to the separate species. This feature can also influence the interspecific relations in a given focus and also in the area to which the parasites disperse from a focus. There is no doubt that a species whose foci can be found in a certain area may be more successful in interspecific relations than a species whose foci are extremely rare or even absent. For example, in C. Europe, parasites of *Aphis fabae* disperse to sugar beet fields from their

foci in the field neighbourhood to attack the aphid that has immigrated to the field. The presence of the foci seems to play a major role as to the parasite action in the field plot, and consequently in interspecific relations in this plot as well.

19. Microhabitat distribution. Although they may occur in the same area, the same kind of habitat, and attack the same host, the parasites are further differentiated with respect to microhabitat, either due to microclimate or ecological niche. Consequently, such a microhabitat distribution also influences their interspecific relations. The most carefully observed example of such relations is that of parasites of *Therioaphis trifolii* (see: v.d. BOSCH et al., 1959, 1964, etc.). Field observations made in the natural home of the parasites, in the Middle East, showed the occurrence of *Trioxys complanatus* in the hot lowlands, *Praon exoletum* in mild areas, and *Aphelinus* sp. in the humid coastal areas. Later, after their establishment in the same plots by the end of 1957 in California, the parasites spread naturally from localized foci over considerable distances in several areas; however, the range of each parasite species differed from that of the others. Such a dependence was supported by observations on the parasite establishment in Arizona (BARNES, 1960), where each of the three species was included in releases made in various areas, however, recoveries showed *Pr. exoletum* to be poorly established and having a low effect; *Tr. complanatus* was well established and became a substantial control agent, while there were no recoveries of *Aphelinus semiflavus*; these results are apparently due to the hot dry climate of Arizona and parasite requirements on the microhabitat. A similar difference as to the microhabitat was recognized by ROSEN (1967) in Israel: *Lysiphlebus fabarum* and *L. ambiguus* were found to be common parasites of *Toxoptera aurantii* on Citrus; however, the first species was most abundant in the northern coastal plain, while *L. ambiguus* was dominant in the southern and central parts of the coastal plain, being entirely absent in the northern coastal plain. As to the significance of ecological niche as a microhabitat, observations of MCLEOD (1937) can be mentioned: In greenhouses *Myzus persicae* lived on most parts of its host plants, *Ephedrus persicae* attacked only aphids that were more exposed, while *Aphidius matricariae* preferred shady situations. Similarly, we have observed apparent differences in *Diaeretiella rapae* parasitization depending on whether the *M. persicae* colonies were on flat and large leaves or on tops of plants in a greenhouse.

20. Habitat distribution is relatively stable in a given part of a geographic distribution area in various parasite species, although habitat dependence can show certain variations in separate climatic zones. Consequently, certain parasite complexes can be recognized inhabiting certain kinds of habitats. In connection with host specificity, seasonal peculiarities, host life-cycle, etc., various interspecific relations can be recognized in the separate habitats.

21. Geographic distribution. Development of aphids and parasites and differences in their relations to the environment caused the present different possibilities of aphids and parasite occurrence as to the general distribution. The same aphid species can be attacked by different parasite species in various parts of its distribution area, or parasites attack the aphid in a part of its distribution area only, etc. In connection with the development of separate parasite faunas, host specificity features, etc., the occurrence of different interspecific relations among separate parasite species in various parts of their distribution area can be seen. Numerous examples can be found in the chapter on Distribution.

Geographic distribution influences also the occurrence and seasonal history of both aphids and parasites. For example, *Aphis fabae* is a dioecious aphid in C. Europe, and two parasite complexes can be recognized which attack it, depending on whether it occurs in the forest or steppe habitats. However, in the southern areas, the aphid is

anholocyclic and a single parasite complex is present there. Similar differences are in *Forda* species, which are holocyclic dioecious in southern Europe and Asia and anholocyclic in C. Europe.

22. Population densities seem to influence interspecific relations among the parasites in two ways: in the frame of a given host species population, low host population means a greater possibility of superparasitism and multiparasitism owing to restricted food sources, although there are other factors preventing these situations, such as dispersal, hyperparasites, etc. If there is a parasite species that reveals a good searching ability under low population density, it may reach high effectiveness under certain conditions, and superparasitism apparently occurs as well; this is the case of *Aphidius ervi* and its parasitization of *Acyrtosiphon pisum* in early spring in C. Europe, where there may be relatively low density of fundatrices that hatched from overwintering eggs, and a high density of parasite population, which overwintered inside the mummified aphids. The other kind of influences of densities on interspecific relations occurs in the case of widely specialized parasites: if a parasite species attacks two to three species of aphids simultaneously in a given habitat, it may become concentrated to two or even a single species due to the emigration of aphids from the habitat; if other species of parasites attack also the aphid species that remained, it could change the interspecific relations in consequence. These seemingly are the cases of parasites of certain dioecious aphids in C. Europe, but they are not satisfactorily known yet.

23. Hyperparasites are known to limit the primary parasite populations to a various degree. Consequently, the hyperparasitized primary parasite populations become less numerous and this can cause changes in interspecific relations as well with respect to parasite effectiveness, dispersal, etc.

24. Community equilibrium influences the interspecific relations in a given community. Parasites and other natural enemies are factors that limit the occurrence of aphids to a certain level, and they themselves are limited by their own natural enemies. Results of FIMENTEL (1961) obtained in mixed and pure stands in Brassica oleracea community showed that there was interspecific competition among the three aphid species present, *Lipaphis pseudobrassicae*, *Brevitoryne brassicae* and *Myzus persicae*, but in mixed stands the aphid species never became sufficiently abundant for any measurable competition. Natural enemies tend to preserve the balance between species populations and to prevent the extinction of one species by competition: *Diaeretiella rapae*, which attacks all the three aphids mentioned, generally parasitized the more dense species to a higher degree than the sparse species. This was apparently due to general pressure of the natural enemies on the more abundant species as the most dense aphid populations had the largest colonies, they consequently were the easiest to be found and parasitized. As a result, the parasites concentrated on the most dense population, and the least dense species were omitted. In the case the three aphid species would be attacked by several parasite species, different interspecific relations would appear in accordance with the density of the separate aphid populations.

Such a regulation, however, is different in different environments, stable and unstable environments exhibiting the most obvious differences.

25. Relations in a community. In a given habitat such as deciduous forest, field meadow, etc., a certain community exists which is principally composed of various food chains. The parasites can be, depending on their host range, seasonal history, etc., members of a single or more food chains in this community. Besides, they can be also members of other food chains in the neighbouring communities. Various relations among the separate parasite species may be recognized in consequence:

A single species of aphids may occur on a plant which may be attacked by a single parasite species: For example, *Brevicoryne brassicae* on Brassica crops is mostly attacked by a single parasite species, *Diaeretiella rapae*, in C. Europe.

On *Euonymus europaea* in spring, however, *Aphis fabae* is attacked by three parasite species, i.e. *Trioxys angelicae*, *Praon abjectum* and *Ephedrus plagiator*.

In other cases, there may be various aphid species on a plant, although only some of them are attacked by parasites. For example, *Juglans regia* in C. Europe: *Chromaphis juglandicola* is attacked by *Trioxys pallidus*, while *Callaphis juglandis* is free of parasites.

Or, an almost extreme case can be mentioned, that of the alfalfa crop in C. Europe, where three aphid species can be found, each of them being attacked by a separate parasite complex, and the separate parasite species have no relation to the other aphids present in the alfalfa ecosystem owing to their host range: *Acyrtosiphon pisum*—*Aphidius ervi*, *Praon dorsale*; *Therioaphis trifolii*—*Praon exoletum*; *Aphis craccivora*—*Lysiphlebus fabarum*, *Lipolexis gracilis*.

26. Other natural enemies. The above factors were demonstrated with respect to aphid parasites. But there are other groups of natural enemies that exhibit their own peculiarities in their biologies, which are different from those of the parasites, and new viewpoints on interspecific relations can be recognized. Apparently, each ecosystem would need a special research to show such interrelations in detail.

27. Control measures. Man's activities may cause severe changes in interspecific relations in aphid parasites as they may favour one species and simultaneously be unfavourable for another species. Introduction of a parasite into a new area is perhaps a classical case; the species must adapt itself in the new environment and new interspecific relations are a necessary part of such an adaptation. Other effects of man's activity may be found in the influence of tillage, cultivation, cutting, treatments, etc., which may exhibit a different role with respect to interrelations in a given community.

28. Relations of factors. It is to be seen from this review that the factors mentioned are far from being equal as to the influence on interspecific relations. Some of them, such as temperature, play a major role, some are less significant. Their action, however, seems to be of a complex character, they mostly condition each other. Consequently, interspecific relations are rather complicated.

29. Relativity of species—superiority. The complex action and different degree of significance of factors influencing the interspecific relations results in the fact that there is no species that would be dominant in all respects: some features are favourable, others indifferent or adverse. The conclusions of FORCE & MESSENGER (1963), based on a comparison of relations of three parasites of *Therioaphis trifolii* seem to be well supported: 'It would seem that the greater the number of criteria selected for basing a judgement of superiority, the more likely are there to be contradictions as to which species will prove superior in nature'.

— ECOLOGICAL HOMOLOGUES. General observations on many parasite species could perhaps show that numerous ecological homologues can be found. For example, it is a common case that several parasite species parasitize the same host in a given habitat. However, it is known that ecological homologues cannot coexist for long in a habitat (see: DEBACH, 1964). Therefore, it is apparent that in nature ecological homologues cannot be found below the level of habitats, the further requirements of the species as to the microhabitat being different, otherwise competition and elimination of one of the species would follow. This state is undoubtedly the result of a long process, during which the present interspecific relations among the parasite species (and other natural enemies) have developed. Although we have a certain number of rather detailed observations on parasite biologies mentioned in various papers, they

do not only deal with the problem of ecological homologues. A single detailed study seems to be presented by different papers of various Californian authors (SCHLINGER & HALL, 1960, 1961, v.d. BOSCH et al., 1959, 1964, FORCE & MESSENGER, 1964, 1965, etc.) on introduced parasites of *Therioaphis trifolii* in California. These parasites at first seemed to be rather related ecologically, but further studies have shown great differences to occur. We have reviewed the papers and listed the various criteria to show the differences, as follows:

Trioxys complanatus (= *utilis*)

Note: The numbers are identical in all the species showing the corresponding criteria, which are named in the first species.

1. Progeny: Biparental. 2. Oviposition at 21°C and 27°C: Rapid, frequent. 3. Searching ability at 21°C and 27°C: Rapid. 4. Discrimination of parasitized and non-parasitized hosts at 21°C and 27°C: It does not really discriminate. 5. Host instar preference at 21°C and 27°C: Low aphid instars. 6. Competition in larval stage at 21°C and 27°C: Somewhat higher at 21°C than at 27°C. 8. Total fecundity at 21°C and 27°C: Highest at 21°C, lower at 27°C. 9. Developmental period, generation time, longevity of adults: Shortest developmental period and generation time, longevity of adults short. 10. Quiescent states: Aestival-hibernal diapause. 11. Seasonal occurrence: Most activity in early spring, and depending on the area, through spring and summer and on into autumn and even winter. 12. Dispersal: Low (see: 5). 13. Habitat: Hot dry areas.

Praon exoletum (= *paltauus*)

1. Biparental. 2. Less efficient in oviposition rate than *Tr. complanatus*. 3. Less efficient than *Tr. complanatus*. 4. Less efficient than *Tr. complanatus*. 5. Higher aphid instars. 6. Very successful. 7. Very low at 27°C. 8. Highest at 21°C, rather low at 27°C. 9. Intermediate in generation time, developmental period, and longevity. 10. Hibernal diapause. 11. Active principally in spring time and late summer and autumn. Hot weather conditions unfavourable. 12. High (Alate aphids, see: 5). 13. Mild areas.

Aphelinus semiflavus

1. Uniparental. 2. Slow. 3. Slow. 4. High discrimination of parasitized and non-parasitized hosts (lack of superparasitism and mostly of multiparasitism). 5. Low aphid instars. 6. Fail to survive. 7. Higher at 27°C. 8. Highest at 21°C, lower at 27°C. 9. Longest generation time and longevity over the entire temperature range; its developmental period was the longest at intermediate temperatures, but was shorter than that of *Pr. exoletum* at low and high temperatures. 10. No diapause. 11. Mostly in winter, hot weather conditions unfavourable. 12. Low (see: 5). 13. Mild humid areas.

Although these criteria in all the species show considerable information, they are far from being complete. Host range and geographic distribution are also not mentioned.

- CONTROL. Biological control program starts with the classification of the given pest aphid species, with respect to the given area. Generally, three possibilities are taken into account, which also influence the interspecific relations among the parasites (and other natural enemies) in a corresponding manner.

1. The pest aphid is native to the given area.

A. Natural food chains: These are the usual results of the natural development of the pest organism in a given environment.

B. Semi-natural food chains: In the case that the native parasites are not too effective, other parasite species can be purposely introduced to raise the total parasite effectiveness.

2. The pest aphid is not native to the given area, but its immigration is of an old date, so that indigenous parasites might or might not have adapted themselves to the immigrant host.

A. SeminatURAL food-chains: They are of two kinds:

Aa. Accidental, originating as a result of conditions occurring in a community. Example: Parasites of *Toxoptera aurantii* in the Mediterranean; the aphid is an apparent immigrant of southeast-asian origin, being spread via Citrus cultivation and importation.

Ab. Non-accidental, if there is a parasite species introduced to raise the total parasite efficiency. Example: This would be the case if *Lysiphlebus testaceipes* would be introduced from Cuba to the Black Sea Coast Citrus area to raise the total parasite efficiency. Example: Introduction of *Aphidius smithi* to California, where *Acyrtosiphon pisum*, an introduced pest, is attacked by secondarily adapted native parasites.

B. Artificial food chains: This would be the case if the indigenous parasites fail in adapting themselves, various parasites being purposely introduced from various areas.

3. The pest aphid is a newly introduced species.

A. Natural food chains. In such a case the original food chain, which may be found in the native home of the pest is transferred to the new country, where there is a lack of native parasites (natural enemies).

Aa. Accidental. The original native parasites are introduced accidentally and simultaneously with the host. Example: *Brevicoryne brassicae* and *Diurictiella rapae*.

Ab. Non-accidental. This would be the case where there exists a lack of native Californian predators, *Therioaphis trifolii* parasites and predators introduced from the Old World to California.

B. SeminatURAL food chains. In such a case, the parasites occurring in a given country have adapted themselves to the new host, and some original native parasites are either accidentally or purposely introduced.

Ba. Accidental. Good examples as yet are unknown.

Bb. Non-accidental. Example: *Therioaphis trifolii* in California. *Praon exoletum* and *Trioxys complanatus* and *Aphelinus* sp. were introduced to California; the indigenous Californian predators, however, being also effective. *Chromaphis juglandicola* in California is a similar case.

C. Artificial food chains. In this case, there are no parasites (natural enemies) in the country of pest establishment, various species being accidentally or purposely introduced. Examples: Both examples of incidental and purpose introductions of parasites can be found in the Oceanic islands (see: Distribution—Hawaii).

— *Indigenous and introduced parasites.* An introduced pest aphid means a new member in a country of establishment. As already mentioned above, new food chains gradually develop there which can be composed of indigenous and introduced species to a various degree. However, in case of an introduced pest species or parasites, a given community must first respond to its presence through mechanisms of community equilibrium; in consequence, new food chains originate. In such chains, the inter-specific relations can be of different value, sometimes a strong competition can appear as well, cooperation not yet being established. Example: *Therioaphis trifolii*, and the relations of its fungus diseases, coccinellid predators and introduced parasites. With respect to indigenous species of parasites, they may be rather effective in a certain period of the year and, consequently, releases of introduced parasites have to avoid such periods (*Acyrtosiphon pisum* and the relation of *Aphidius ervi* to released *A. smithi* in Czechoslovakia), in other cases, the native parasites are not effective even in a part of the season, so that timing of the release of introduced parasites can be

carried out irrespective of their action (*Hyalopterus pruni* and its introduced parasite, *Aphidius transcaspicus*, in Czechoslovakia).

— Sequential parasitism means a case when an attack by two or more parasite species occurs in consequence of the developmental stages and instars of a host (FLANDERS, 1965). Consequently, the parasites exhibit various relations in such a case. However, sequential parasitism does not occur in the aphids. Their developmental cycle is too rapid to enable the development of separate parasite species that would develop during one aphid instar. Some parasites prefer certain aphid instars, but sequential parasitism in such cases can mean only superparasitism and/or multiparasitism as only a single parasite larva completes its development.

Multiple introduction. Interspecific relations seem to be just important in some problems of parasite introduction in a biological control program. Generally, two viewpoints are recognized:

1. DEBACH & SUNNBY (1963) consider multiple introductions to be advantageous in biological control,

2. TURNBULL & CHANT (1961) consider that the more species of agents that attack the sooner competition will start and the more severe will be its effect; consequently, it is recommended to avoid large numbers of parasite species.

These opinions will be discussed in the chapter on biological control in more detail. With respect to interspecific relations, we can only point out that the state that occurs in nature must be our guide in a parasite introduction program as well: Natural food chains are composed of groups of various predators and parasites, never from a single species; their action is basically complementary.

REFERENCES. 10, 21–2, 45, 90, 114–6, 125, 126, 128, 129, 158, 160, 252–6, 268, 291, 301, 356–9, 364, 399, 402, 417–9, 421, 425, 450, 471, 484, 502, 510, 540–1, 646, 688, 702, 705, 748, 767, 806, 826, 894–5, 946, 971, 997, 1003, 1005, 1019, 1034, 1062, 1072, 1101, 1163, 1189, 1233, 1238–9, 1273, 1281.

Aphid-attending Ants

The relation between ants and natural enemies of the Homoptera represents a special topic. As the natural enemies of Homoptera do not constitute a homogeneous group but belong to various insect orders, we shall deal here only with aphids and associated insects due to the scope of this book, the rest of the Homoptera like coccids, etc., not being considered. As a result of the rather intensive investigations of the aphid predators, their relationship to ants seems to be known at least regarding the basic features, while the aphid parasites, due probably to the rather poor knowledge of their taxonomy and ecology, have been left almost untouched except for some cases mentioned below.

To illustrate the inadequateness of opinions and their accidental selection, a short review of papers dealing with aphid-and-aphid parasite association is given below.

— Attendance by *Lasius*-ants. EL-ZIADY & KENNEDY (1956): Occasionally, the *Lasius* sp. ants appeared to notice and 'run at' adults of a parasite, *Aphidius* sp. (probably *Lysiphlebus fabarum*—author's note). Ant attended aphid: *Aphis fabae*.

BANKS (ref. after WAY, 1963): The ants *Lasius niger* L. disregarded aphid parasites. Ant attended aphid: *Aphis fabae*.

PONTIN (1955): *Aphidius* sp. were not noticed by *Lasius niger* L.

WICHMAN (1955): *Aphidius* sp. were not noticed by *Lasius niger* L.

BANKS (ref. after WAY, 1963): He even found the ants *Lasius niger* L. palpating

Aphidius sp., while they were ovipositing in aphids. Ant attended aphid: *Aphis fabae*.

PONTIN (1960): points out that there must be a selection pressure favouring ant-tolerated predators and parasites such as the aphid parasite *Paralipsis enervis*, which adult is fed by regurgitation from *Lasius niger* workers and by aphid honey-dew obtained in both instances by ant-like association (HINCKS, 1958, after PONTIN, 1960).

ROTHSCHILD (1963), when studying some aphids and their parasites on fruit trees in Gr. Britain, observed that aphid colonies attended by ants (species not identified) were unparasitized, neighbouring colonies free of ants were heavily parasitized (aphids: *Hyalopterus pruni*, parasite—*Ephedrus plagiator*, *Praon volucre*; *Aphis pomi*, parasite—*Trioxys angelicae*).

— Attendance by *Formica* ants. WELLENSTEIN (1957) emphasized that the parasites (*Aphidius* sp., *Trioxys* sp.) kill inadequately tended surplus aphids that are not needed by ants. He indicated experimentally that the mentioned parasites were disturbed by the ant activity but not attacked. He also demonstrated the importance of root chambers where the same aphid species as occurred above ground are free from parasites.

MASON (1922) gives two cases of ant (probably *Formica* sp.—author's note)-aphid parasite relationship: *Xenostigmus bifasciatus* (ASHMEAD): a very abundant and effective parasite (of *Cinara* spp.—author's note) and occasionally was observed ovipositing in the aphids. It would fly to a branch on which the aphids were feeding and approach the colony cautiously within a close range, then make a quick rush towards them, twist the abdomen between and under the legs, quickly pierce the aphid with its ovipositor and run back. If undisturbed, it would repeat this practice several times. However, the ants which usually attend these aphids would often watch for this invader and drive him off before he reached the aphids. The parasite also appeared to be afraid of the ants. Ants also protect them (*Cinara* spp.—author's note) by driving away their parasites and predatory enemies. The most noticeable defense was a sort of cover built over them by the ants. The primary purpose, probably, was to keep parasites away but it would also serve as protection against cold and storms... Thus aphid never occurs in large numbers probably due to the high percentage of parasitism. Its large size makes it an easy prey for hymenopterous parasites.

— Attendance by undetermined ants. According to ULLYETT (1938) ovipositing ♀♀ of *Diaeretiella rapae* (= '*Aphidius* sp.') are disturbed by ants in their efforts to protect their hosts; in a colony, where ants are numerous, the efficiency of parasites is decreased and the colony continues to flourish. The efficiency of *Diaeretiella* is in inverse ratio to the prevalence of ants.

HILLE RIS LAMBERS (in a letter) suggested that there is a record on a direct attack of ants on parasite mummies known from C. Asia, the aphid being perhaps *Pterochloroides persicae*; unfortunately, we have been unable to find the paper mentioned.

STARÝ (1966) summarized his original observations and showed that generally there is no ant influence on aphid parasites, many examples being mentioned (details, see below).

The results can be summarized as follows:

a) The different cases studied are quite occasional, without any respect to different groups of aphids and parasites.

b) In all cases there is a lack of knowledge of parasite group ecology, which is caused by the lack of such data in general at the corresponding period.

c) Only *Formica*- and *Lasius*-ants are practically dealt with.

— APHID - ANT RELATIONSHIP. The following three types of aphid-ant relationship can be recognized:

1. Constant, if it is continuous and results in adaptations both in morphology and ecology of the aphids.

2. Temporary, if the aphids are attended by the ants for the whole season or for a part, the relationship forms without resulting in apparent morphological or ecological adaptation.

Many holocyclic dioecious aphid species might be cited as examples. They occur in spring on certain plants (trees), being attended or unattended by the ants there, in summer they migrate to stems and leaves of other plants, where the ants do or do not attend them. In this case the relation between the ants and aphids is not a very close one.

3. Facultative, if the ants meet or occur in the colonies of aphid species belonging to this type quite occasionally and have no relation to them. This is a common case.

Of the three groups, apparent adaptation has developed in the aphids belonging to the first group only. These aphids, being closely associated with ants, have in general poorly developed structural modifications, which may be used for the defense against the natural enemies, when compared with unattended aphids (cornicles, dense wax filaments, heavy sclerotization of cuticle, saltatorial legs, etc.) Similarly, the constant aphid-ant relationship requires a certain type of aphid's life cycle. The obligatory host alternation, which occurs in the holocyclic heteroecious species, prevents a continuous association with ants, although the aphids may be attended by ants either on primary or on secondary host plants, or on both, while the holocyclic monoecious and anholocyclic species can continuously associate with the ants.

— GROUPING OF PARASITES. From this viewpoint, the parasites may be divided as follows:

— 1. *Parasites of ant-unattended aphids.* This is quite a numerous group including many species whose hosts have no relation to ants, e.g.: *Dyscritulus planiceps*, *Trioxys cirsii*, *Monoctonus pseudoplatani*—all being parasites of *Drepanosiphum platanoides*. Further, *Aphidius funebris*, *A. absinthii*, *Praon dorsale*, *Pr. absinthii*, *Ephedrus campestris*, *Trioxys centaureae*, *Tr. pannonicus*, etc., all of them are parasites of certain Dactynotinae aphids (*Dactynotus*, *Macrosiphoniella*, *Titanosiphon*, etc.). If parasites of this group meet an ant in or near the host aphid colony, it is an occasional meeting and it cannot be generalized as to the mutual behaviour.

— 2. *Parasites of ant-attended aphids.* This group can be subdivided:

— a. *Non-specialized parasites* (Figs. 268, 269) — Their relation to ants depends more or less on their behaviour in relation to aphid hosts, and it can be considered analogous to other responses evoked by the mechanical stimuli coming from the environment.

As mentioned above, the morphological and ecological adaptations for defence against natural enemies are rather poor in ant-attended aphids. A behaviour that would correspond to that of the host would be expected to develop in the parasites, too. This is really true in the parasites of these aphids; the behaviour being typical in a long act of oviposition, negation of weaker mechanical stimuli, etc.

Lysiphlebus fabarum, a common parasite of various aphids (*Aphis*, *Brachycaudus*, etc.) in Europe: we observed its behaviour in an *Aphis fabae* colony on *Cirsium* sp. The aphid colony was numerous, the percentage of dead, mummified aphids was high. The colony was densely occupied by *Lasius niger* ants and there were about eight adult specimens of parasites present, which had newly emerged, attacked intensively and oviposited in instar II and III of the aphids. The ovipositing parasites were often tapped by the ants' antennae, but they laid eggs without interruption, the oviposition lasted for about 40 sec as usual. The ants' behaviour was indifferent and the parasites were tapped in the same manner as the aphids. But when disturbed by our slightly beating the plants with a pincette, the parasites were quite indifferent and oviposited



Fig. 268. *Aphis* sp. on *Peucedanum alsaticum* root-collar. Runs of *Lasius-anis*.

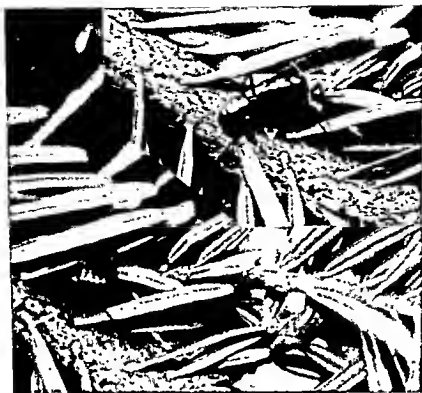


Fig. 269. *Cinara* sp. on *Abies alba*. Inset: ant-attendance.

—which is their usual behaviour in such cases—while the ants responded in a completely different way, assuming a defensive attitude and shielding the aphids.

This type of relation between ants and aphid parasites can be confirmed by a similar case, observed in the colony of *Chaitophorus* sp. on *Populus tremula*. The colony of aphids was strongly parasitized (many mummified aphids present) by *Lysiphlebus salicaphis*. The adult parasites, probably newly emerged from the mummies, moved in the colony and infested and oviposited in the aphids. Two ant species—*Lasius* sp. and *Formica* sp., species of a very different behaviour,—occurred in the colony. The ants of both species tapped the adult parasites with the antennae, and they did not seem to be disturbed. When the plant was slightly beaten with the pincette, the ants reacted immediately, and, especially *Formica* ants, assumed an aggressive attitude.

It results from our observations that the ants are indifferent to the aphid parasites, and shield them and the parasitized (both still living and dead mummified) aphids from strong adversory stimuli. The degree of parasitism of aphids by parasites does not depend on the presence or absence of ants, as the parasites disregard them. On the contrary, the ants shield even the colonies with a high percentage of dead mummified aphids. From this point of view the importance of aphid parasites is even greater.

- b. Specialized parasites — In the parasites of this group, besides the parasitism on aphids attended by ants, a particular relation to the ants has developed that can be considered as a case of mutualism (Fig. 270):

Paralipsis enervis may be taken as a representative of this group. The ants behave to the adults of this parasite as to other symphyla, palpating them; regurgitation was observed, too. Besides, the ants mutilate the wings of parasites as it is usual in other cases of mutualism. The close relationship of *P. enervis* to the ants is apparent also in



Fig. 270. *Paralipsis enervis* fed by *Lasius*-ant (after MANEVAL, 1940).

its morphological resemblance to the genus *Lasius*. Evidently, this is a close adaptation to the most abundant aphid attending ant species, as *P. enervis* parasitizes quite a number of root aphids of various groups, which are attended by *Lasius niger* particularly. Moreover, the movements of the adult parasites are typical, too—the abdomen bent down in a specific way is quite unusual in the aphidiids, suggesting a complete adaptation of the parasite to the ant nest environment. *P. enervis* also hibernates in the adult stage in *Lasius*-nests, while the other aphidiids overwinter in the prepupal stage inside mummified aphids. This is also an adaptation to the nest life and ant nest environment, as many species of underground aphids cannot survive the winter except with the ants that are apparently adapted to tending them.

As the wings of the *P. enervis* are mutilated the parasite ♀ is unable to fly off and search for the aphids in other environments. Its dispersal is secondarily restricted to the first visited ant nest and depends on the dispersal of the underground aphid species which in turn are dependent on ants in dissemination. This is of course not true of the newly emerged ♀♀ of the parasite that fly and disperse on longer distances and attack a number of various root collar and root aphids.

All morpho-ecological adaptations mentioned are well visible in the food specificity of the parasite, as it attacks a number of root aphids attended by ants, if they live in the underground ant chambers or inside ant runs (or shelters) around root collars of various plants.

Nevertheless, the fact must be stressed that *P. enervis* has to be classified primarily as a parasite specialized to the parasitization of root aphids, being from this point of view an equivalent to parasites of gall-producing aphids, leaf-curling aphids, etc. The close attendance of the parasite by the ants is a secondary character that developed during the long contact with root aphid environment to which also the aphid attending insects belong. This is stressed by the ability of *P. enervis* to occur and parasitize root aphids unattended by ants, mummified aphids and parasite ♀♀ with unmutilated wings being found in this case.

To illustrate the above mentioned generalized notes on the relation of parasites to aphid attending ants, some selected results of our field observations made in Italy (STARÝ, 1966) may be mentioned. During these observations, we collected all the ant species in aphid colonies. The aphid colonies were then put in vials to rear parasites. Although the samples taken mostly do not represent the typical ant-attended aphid species, temporary ant-attendance being most common, it is recognizable from this material, that the aphid colonies included both parasitized and unparasitized aphids, whether the ants were present or not. Similarly, the same can be said of all the secondary parasites—the Charipine cynipids, the proctotrupids (*Lygocerus*) and chalcids (*Asaphes*, *Pachyneuron*, *Conina*, etc.). The results obtained in this way show that the aphid colony (*Chaitophorus*, *Aphis*, etc.) were often attended (or visited) by two or three species of ants of a very different behaviour (*Formica*, *Lasius*, *Crematogaster*, *Iridomyrmex*, *Pheidole*, etc.). Nevertheless, parasites were reared from these colonies that were later collected. This fact stresses further our observations mentioned previously that the ants disregard the parasites, otherwise parasitized aphids could hardly be found in a colony attended by three different ant species. Similarly, the following results can be obtained from summarizing the parasite-ant list: certain aphid parasites, because of food specificity factors, are typical of certain aphid groups, being reared from colonies by ants attended or visited irrespective of the presence or absence of ants, of the number of species or specimens of ants present.

— Aphid attending ants and parasites. The following three kinds of relations of ants to aphid parasites may be recognized:

1. Relation of aphid attending ants to parasite adults. As our observations have shown the ants ignore the presence of the adult aphid parasites in the attended aphid colony. It results that the parasitization of aphids in the open does not depend on the presence or absence of the ants, this being determined by other factors. That is why adaptation has developed in the parasites only of a secondary character (like mutualism in *Paralipsis enervis*—*Lasius* sp. case).

The ants protect (see WAY, 1963) the aphid colonies from the natural enemies (predators). But because they ignore the presence of adult parasites in the colony, they thus indirectly protect the parasites, too, safeguarding their more or less undisturbed oviposition and thus increasing the percentage of parasitism (Fig. 270).

2. Relation of aphid attending ants to mummified aphids. In a certain stage (last instar) of its development, the larva of the parasite kills the aphid, spins the cocoon inside the empty aphid skin, fastens it to the surface of the leaf and pupates. Such aphids are clearly recognizable in the aphid colony and they are generally called 'mummified'.

The ants usually attend the mummified aphids similarly as the other living aphids (Fig. 271). There is only one exception known, that of *Lasius fuliginosus* LATR. This ant species attends, among other aphid species, also the *Stomaphis* spp. aphids that are infested by the parasite *Protaphidius wisniamii*. In this case, the mummified aphids are nibbled by the ants (Fig. 272), so that only a shiny ball, the true parasite cocoon, remains. But the ants protect this cocoon in a similar way as they do the living aphids.

3. Relation of aphid attending ants to living parasitized aphids. The parasitized aphid, containing an egg or lower instar parasite larva, is not recognizable in the colony. It moves and feeds in the usual manner. Gradually, as the parasite larva develops, the movements of the aphid are slower and at the end it is killed by the parasite (see above). No differences in behaviour of the ants to healthy or parasitized aphids have been observed.

— Parasite specificity. If we compare the ant attended aphid groups and their parasites with respect to the factors influencing the host range of the parasites (see: Host



Fig. 271. *Aphis schneideri* on *Rabes nigrum*, ant-attendance by *Lasius*-ant. The colony is heavily parasitized by *Lysiphlebus ambiguus*.

specificity), it is obvious that the ant attendance of the host aphids does not influence the host range of parasites, although secondary adaptation in parasite behaviour may develop in some cases.

From this point of view, the aphid behaviour has the most important role, the parasite being adapted on it, similarly as in the case of the mode of aphid life, of habitats, etc.

A strict attendance of aphids by ants and their defence against parasites would surely cause an elimination of certain species or groups of aphids that would not be attacked by parasites. We know some cases when a certain group of specialized ant attended aphids (*Trama* spp.) is not parasitized, better to say, we still do not know any aphidid parasite infesting it. But such cases are believed to be the result of either poor knowledge of parasites of a certain group, or, as in other cases in unattended aphids, a certain group of aphids may be free of aphidid parasites in general. This depends on a number of other factors. Generally, in accordance with the ecology of the parasites, we can say that the aphidids are today mostly connected with free-living aphids, leaf-curling and gall producing aphids etc., while the true root aphid species are parasitized by a comparatively low number of parasite species.



Fig. 272. *Protaphidius wissmannii*, mummified *Stomaphis quercus* aphid. From left to right: gradual nibbling of the aphid skin by *Lasius*-ants, the true parasite cocoon remaining at last.

- Relation of parasites to ant-runs. There is no doubt that the runs built by the ants around the colonies of root collar aphids namely, have a great importance for controlling the humidity, temperature, etc., favouring the aphid colony development in this way. Nevertheless, there exist certain viewpoints in the literature (see Chapter III) that these runs have also the significance (or their main role) of protecting the aphids from the natural enemies. As our numerous observations have shown, this is not true in the case of parasites. The parasites are able to attack aphids also inside the runs, using probably certain holes in the runs to invade it, or they are specialized for such a kind of life (*Paralipsis*) apart from the period of high temperature and humidity, when the aphids spread out of the runs all over the plant as in the case of numerous aphid species living on root collars in spring (Figs. 253, 268).

- NATURAL LIMITATION. Observations of various authors have shown that in consequence of the ants' activity, i.e. increasing the environmental capacity for the attended aphids by removing honeydew or excavating galleries around suitable feeding sites, the aphids can remain in favoured parts of the plant for a longer time and in a larger number than in the absence of ants.

The ant-aphid-parasite association may be, in certain cases, suitable for the natural limitation of aphids. As mentioned above, the aphid parasites are disregarded by the ants. It follows that the aphids are parasitized by the ants present or not. In view of an increased degree of parasitism, which is, however, influenced by a number of other factors not mentioned here, the attendance of ants means a possibly prolonged occurrence of the aphids on a certain plant in a certain habitat, higher rate of multiplication, delayed production of winged forms, etc. (comp. EL-ZIADY & KENNEDY, 1956, JOINSON, 1959), and thus a theoretical possibility of the aphid limitation by the parasites. If we do not consider the occurrence of ants as attendants of the aphids on cultural plants, where the protection of the aphids from predators could have a negative effect, the aphid-ant relation is actually advantageous in view of the natural limitation of aphids by parasites. Particularly if the aphids on the primary host plants are heteroecious, the relation to ants means a longer stay on the primary host plants. Since the aphids (in connection with the temperature they require for reproduction) are usually numerically much stronger than the parasites, such a prolonged stay of the aphids is advantageous if the parasites occur, as it means a longer contact pos-

sibility of the parasites with the aphids, i.e. increased parasitization and decreased number of aphids migrating to other habitats (particularly of the steppe type), often on cultural plants.

The close relation of the parasites to the ants, as in the case of *Paralipsis enervis*, is supposed to be less suitable for the dispersal and effectiveness of the parasite, since the wings of ♀♀ are mutilated by ants, the dispersal of the parasite is secondarily limited to one ant nest, from which it can spread to the nearest neighbourhood only. But since *P. enervis* was sometimes found to be a rather effective parasite species, its life-history in relation to the influence and dispersal of newly emerged parasites from the ant nest in particular should be further studied, as it is the commonest of the few parasite species that can attack the underground aphids.

— BIOLOGICAL CONTROL. The aphidiid parasites have been used as biological control agents practically only in the past few years. Unfortunately, in all of the three generally known cases of useful biological control—*Therioaphis trifolii*, *Acyrtosiphon pisum* and *Chromaphis juglandicola* the aphids do not belong to ant-attended species, so that allied problems of introduced parasites-ant relationship, etc., were not dealt with.

Nevertheless, according to our observations, the following points have to be stressed in respect to biological control:

1. The aphid parasites are indifferent to ant-attendance in the aphid colony. Similarly, the aphid-attending ants disregard the parasites.
2. Morpho-ecological adaptation of parasites due to the ant-attendance of the host aphids, if developed, are of a secondary character. The presence or absence of ants is not an important factor controlling the parasite effectiveness.
3. The ant-attendance of aphids does not seem to influence the parasite specificity.
4. The ant-attendance of the pest aphid controlled has, however, to be kept in mind when evaluating the ecological characteristics of different species of parasites before attempts of an establishment are made.

The peculiarities of the relation of aphid parasites to ants may have a practical significance in biological control of aphids. As has been mentioned by various authors (see: WAY, 1963), predators are often attacked by aphid-attending ants, aphid colonies being protected in this way from the predators attack. On the other hand, as our observations (STARÝ, 1966) have shown, aphid-attending ants ignore the parasites. Theoretical conclusions may be made in consequence that in case the effectiveness of predators is limited by the ants, biological control agents effective enough and not attacked by the ants should be used. Just the parasites seem to be a suitable group. Moreover, as the ants remove honeydew from the aphid colonies and favour the conditions of the aphid colony, they simultaneously prolong the aphid presence on a plant and enable better effectiveness as well, as the latter is usually the greatest just before the aphids emigrate from the plant.

One apparent example of such biological control activities can be mentioned—*Aphis gossypii* as a cotton pest in tropical Africa (PEARSON 1958). This aphid became a serious pest on cotton. Although it had been at first a pest of minor significance, its outbreaks followed apparently the use of insecticides when other pests were under control. As one of the factors affecting the prevalence of the aphid pest, which was demonstrated in Africa, is ant-attendance. Well-defined patches (watering of plants) in which young cotton plants were annually heavily infested by aphids were shown to centre on nests of the ant, *Myrmica natalensis* (F.S.M.), which fosters *Aphis gossypii*, feeding on its secretion and appearing to destroy *Syrphid* larvae (PEARSON 1958). As almost no parasites have been observed to attack *A. gossypii* on cotton in Africa except one rare case, the introduction of effective parasite

species from climatically related countries could be useful due also to the peculiarities in parasite behaviour to aphid-attending ants.

INTEGRATED CONTROL. A similar aspect as that on biological control of aphids and ant-attendance may be applied also in the integrated control basic research.

The contemporary situation in this respect has been recently summarized by DE FLUITER (1966) when dealing with aspects of integrated control with reference to aphids and scale insects: 'colonies of aphids and scale insects are often visited by ants feeding upon excreted honey-dew. Sometimes the ants afford protection to aphids and scale-insects by preventing them from being parasitized, eaten by predators or infested by pathogens. Where the ants are controlled, predators, parasites and pathogens have a free access to the colonies to destroy them rapidly. In other cases the ants manifest their ownership by carrying the aphids or scale insects away when the nests are disturbed, or by actually breeding them on roots in their nests or in the neighbourhood. Then the control of the ants may result in a collapse of the aphid or scale insect population.

Although the mentioned summary is too general, there is no doubt that the peculiarities of aphidiid parasites-aphid-attending ants relationship may apparently somewhat modify the integrated control of the ants program.

REFERENCES. 26, 38-41, 50, 84, 99, 146, 148, 225, 238, 282, 288, 308, 314, 321-2, 389, 394, 400, 409, 452-3, 460-1, 481, 522, 536-7, 570, 598, 600, 618, 624, 704, 719, 732, 772, 781, 791, 793, 795, 827, 840, 845, 872, 901-3, 919, 929, 945-6, 947, 1007, 1013, 1110, 1125-6, 1238, 1276, 1288, 1301, 1338-9.

Natural Enemies

Like every group of animals the aphidiid wasps can be attacked by various natural enemies. This can be either due to interspecific relations between the primary parasites, or primary parasites and predators, or the natural enemies may be obligatory agents that limit the numbers of the aphidiids as primary parasites of aphids. We have decided to restrict ourselves to a short review of the natural enemies of the aphidiids, as according to our opinion another book could be written about each group of the obligatory natural enemies of the aphidiids, the relations to the aphidiids will be even more complicated as the level of relation between primary parasites and hyperparasites is a higher one. Some observations, such as those of BROUSSAL (1966) at least partially, initiated in showing these complicated relations.

1. Entomophagous fungi. A descendent stage of an aphid colony as well as cooler and rainy periods of the season can often be observed to be followed by an appearance of fungus disease. Fungus disease can reduce the aphid numbers considerably. Weather conditions enabling the rapid dispersal of a fungus disease seem to be more useful for aphid control than the appearance of the disease at the descendent stage of an aphid colony, as in the latter case mostly the remaining aphids that did not emigrate or were not eaten by natural enemies, are reduced. Fungus disease apparently infests both healthy as well as living parasitized aphids. Even the infestation of parasitized mummified aphids is mentioned in the literature (LYLE, 1918). However, the infestation of parasitized aphids is only an occasional phenomenon. Fungus diseases can infest all the aphids present in a colony, consequently, they must be classified as facultative enemies of the aphidiid parasites.

2. Aphid predators represent a numerous group of insects. Some Acari of the

thrombidid group can often be observed to attack aphids, in more humid microhabitats for instance. Some Neuroptera are common aphid predators. Many species of the families Chrysopidae and Hemerobiidae may feed obligatorily on aphids, both in larval and adult stage. The order of Thysanoptera includes also some predatory groups which are known to feed also on aphids. Some groups of the Heteroptera, for example the anthocorid, mirid, and nabid groups, represent aphid predators as well, both in nymphal and adult stage. The Coleoptera include a numerous group of the Coccinellidae many species of which represent obligatory predators of aphids both as larvae and adults. Some groups of the hymenopterous superfamily Sphecoidae are also aphid predators. The adults collect aphids from colonies and use them as food for their larvae in underground nests. Of the Diptera, there are three groups, the Syrphidae, Itonididae and Chamaemyidae, which include many aphid predators. These species are predatory in larval stages only, while their adults do not feed on aphids. Besides these mentioned groups, which are mostly obligatory predators of aphids, there is a number of aphid predators, which are, however, more or less facultative. Some Orthoptera, staphylinid or carabid beetles can be mentioned. As to the higher groups of animals, some birds and mice are known to feed on aphids, too. All these groups of predators, both obligatory and facultative feeders, do not seem to distinguish between healthy and parasitized aphids and thus they represent facultative predators of the aphidid parasites. Nevertheless, none of them is an obligatory predator. As to the dead mummified aphids, they may be devoured facultatively by various predators. We have observed chrysopid larvae attacking the aphid mummies and feeding on the developmental stages of the aphidiids contained in them. Apparently, all the groups of aphid predators which have strongly sclerotized mandibles, can feed on aphid mummies, while dipterous larvae are unable to do so. The degree of infestation of living and mummified aphids is perhaps due to the degree of exploitation of food sources. If the aphids are numerous, living aphids are apparently preferred. However, when aphids are scarce due to emigration, natural enemy action, etc., the larvae of predators which disperse very slowly in search of the host, consequently feed on all the 'aphid-like' sources, including the mummified aphids.

3. Aphid parasites. In the aphid parasites, which represent enemies of the aphidids, we can distinguish two groups:

The first group, which includes primary parasites of other groups such as the Aphelinidae, does not represent natural enemies of the aphidiids in the strict sense of the word, they occur only as their enemies in case of interspecific competition (multiparasitism, etc.).

Another group of aphid parasites includes all the hyperparasites of aphids. They are obligatory hyperparasites of the aphidids during their development, their adults being freely living insects; therefore, they are typical parasitoids, as the aphidids are.

There are three main groups of the Hymenoptera which include the hyperparasites: the chalcids (Pteromalidae) and the proctotrupids (Ceraphronidae) include ectoparasites of the aphidid last instar larvae and pupae, while the cynipids (Charipinae subfamily) are endoparasites of the aphidid larvae. Consequently, various relations can occur among these hyperparasites, either secondary or even tertiary parasitism being distinguishable (see: interspecific relations).

All the groups of hyperparasites mentioned pupate inside the aphidid cocoon, which is either inside or under the parasitized aphids. Their presence may be easily recognized by the shape of the emergence hole, which has irregular margins, and it can be thus easily distinguished from that of the aphidids which is circular, often bearing a lid.

There is one basic aspect that is applied with respect to the natural enemies of the

aphidiids and aphid limitation: the aphidiids are primary parasites of aphids, they consequently represent one of the components of the aphid-natural enemies food chains. Therefore, as they participate in the limitation of the phytophagous insects, i.e. the aphids, they themselves must be limited through the action of their own enemies, the hyperparasites; the interspecific relations between the primary natural enemies are another part of the question; both the degree of action of hyperparasites and primary natural enemies of aphids is regulated by the equilibrium of a given community. Although all the natural enemy groups exhibit a similar pattern in all the communities, it is apparent that certain communities owing to their specific features show a certain prevalence of a given group of natural enemies, although its influence on the aphid numbers is regulated by the community level. For example, fungi may generally be found to be rare in the field communities of the temperate zone of Europe during drier and warmer periods and to be common in autumn when the day is shorter and weather is colder and more humid. However, typical conditions rather similar to those described occur continuously in some of the tropical communities (mountain tropical rain and cloud forest) where we observed a common occurrence of fungus diseases of aphids (Cuba) in a rather more significant way than in other communities of the same area.

It seems necessary to stress one aspect as to the relation of the aphidiids and their hyperparasites. In a similar way as the primary parasites are useful for their hosts, the aphids, in limiting their numbers and preventing overpopulation and the resulting exhaustion of food sources, the hyperparasites must be kept as being useful for their hosts, the primary parasites as well in a similar way. When the primary parasites are not limited by their hyperparasites, their numbers gradually grow higher and overpopulation follows. Although dispersal is one of the means that prevent the elimination of a parasite species in a given plot through overpopulation and exhaustion of food sources, it is apparent that the hyperparasites act in a similar way, although the result of the action of hyperparasites is different—they kill the primary parasites contrary to the dispersal of healthy primary parasite adults from a given plot. In a short given period, it is the same for the community level, whether a parasitized aphid is hyperparasitized or not as it is killed in both cases; however, the next period of aphid-primary parasite relation may be influenced in a different way. The interactions of the host aphid, primary parasite and hyperparasite seem to be best apparent in host-parasite systems in laboratory conditions as mentioned by WAY (1966): In systems containing only *Brevicoryne brassicae* and *Diaeretiella rapae*, the host was quickly eliminated when parasite dispersal was prevented, but with dispersing aphids and primary parasites removed, an oscillating host population has been maintained for over 300 days; there are indications that *Chorips* sp. hyperparasites damp such oscillations (laboratory).

Natural enemies of the aphidiids have to be taken into account in aphid control. Laboratory rearings of primary parasites must be kept in pure culture to prevent an introduction of a secondary parasite or even a predator. Similarly, strict quarantine measures must be applied when shipment of introduced material is received and put into the quarantine laboratory for rearing, as often aphid mummies are sent which contain both primary parasites and hyperparasites. Pure cultures are easier to obtain in laboratory rearing rooms, where an introduction of a hyperparasite from outdoors can be prevented. There is a greater danger of accidental introduction of a hyperparasite to pure culture reared in a greenhouse. Care must be taken as to the development of entomophagous fungi in the rearings. Where there is no controlled photoperiod, as in a greenhouse, the fungus disease usually appears in autumn in the temperate zone (short day, humid and cooler conditions, etc.), and may reduce the

rearings considerably; the best protection of the rearings seems to be the controlled photoperiod and temperature conditions.

The action of hyperparasites is generally considered to be harmful as they can reduce the numbers of primary parasites considerably and cause a decrease of their action. Some authors (e.g. PAETZOLD & VATER, 1966) even mentioned some measures to lower the degree of hyperparasite effectiveness. Nevertheless, according to our opinion mentioned above, the action of hyperparasites must be classified first as a necessary part and law of the community equilibrium level. It seems perhaps better to have their necessary action in mind and develop a corresponding measure in an integrated control program. Better to say, the decrease in aphid parasite numbers does not mean that there will be a temporary lack of a controlling factor, as it is known that because of co-operation, other natural enemy groups may increase as to their action in a corresponding way (see: interspecific relations, natural limitation).

REFERENCES. 157-8, 301, 343, ~4, 377, 421, 512-14, 535, 646, 680, 730-1, 789, 806, 807, 854-6, 1125, 1278-9.

Phylogeny

The aphidiid parasites have apparently originated from the braconoid groups of the ichneumonoid complex of the Hymenoptera. Although they are closely connected with the archaic groups of the recent family Braconidae, with the subfamily Euphorinae namely, they represent both morphologically and ecologically a strictly defined group which cannot be included in the Braconidae. The strict separation of the whole aphidiid group to the parasitism on aphids shows the apparently ancient character of this relationship, stressing the separation of the aphidiids as a separate family of the parasitic Hymenoptera.

A REVIEW OF FOSSIL GENERA AND SPECIES

Genus: *Ephedrus* HALIDAY, 1833.

† *E. primordialis* BRUES, 1933 (Baltic Amber).

† *E. mirabilis* TIMON-DAVID, 1944 (Bass. de Marseille, Oligocene).

Genus: † *Protephedrus* QUILIS, 1940.

† *P. terciarius* QUILIS, 1940 (Haut Rhin, potassium layers, Tertiary-Oligocene).

Genus: † *Propraon* BRUES, 1933.

† *P. cellulare* BRUES, 1933 (Baltic Amber).

Genus: † *Archipraon* STARÝ (in litt.).

† *A. gausai* (QUILIS M.P., 1940) (Haut Rhin, potassium layers, Tertiary-Oligocene).

Genus: † *Praeaphidius* STARÝ (in litt.).

† *P. macrophthalmus* (BRUES, 1933) (Baltic Amber).

† *P. microphthalmus* (BRUES, 1933) (Baltic Amber).

Genus: † *Holocnionus* QUILIS, 1940.

† *H. braconiformis* QUILIS M.P., 1940 (Haut Rhin, potassium layers, Tertiary-Oligocene).

Genus: † *Pseudaphidius* STARÝ (in litt.).

† *P. cenozoicus* (QUILIS, 1940) (Haut-Rhin, potassium layers, Tertiary-Oligocene).

† *P. fossiliferus* (QUILIS, 1940) (Haut-Rhin, potassium layers, Tertiary-Oligocene).

† *P. lysiphleboides* (QUILIS, 1940) (Haut-Rhin, potassium layers, Tertiary-Oligocene).

† *P. nigrofascies* (QUILIS, 1940) (Haut-Rhin, potassium layers, Tertiary-Oligocene).

† *P. oligoarundinis* (QUILIS, 1940) (Haut-Rhin, potassium layers, Tertiary-Oligocene).

† *P. oligocenus* (QUILIS, 1940) (Haut-Rhin, potassium layers, Tertiary-Oligocene).

† *P. premedicaginis* (QUILIS, 1940) (Haut-Rhin, potassium layers, Tertiary-Oligocene).

† *P. pseudogranarius* (QUILIS, 1940) (Haut-Rhin, potassium layers, Tertiary-Oligocene).

† *P. saliniferus* (QUILIS, 1940) (Haut-Rhin, potassium layers, Tertiary-Oligocene).

- † *P. tonieli* (QUILIS, 1940) (Haut-Rhin, potassium layers, Tertiary-Oligocene).
 Genus: † *Oligoaphidius* QUILIS, 1940
 † *O. sannioniensis* QUILIS, 1940) (Haut-Rhin, potassium layers, Tertiary-Oligocene).
 Genus: † *Protodiaeretiella* STARÝ (in litt.).
 † *P. berlandi* (QUILIS, 1940) (Haut-Rhin, potassium layers, Tertiary-Oligocene).
 Genus: † *Protacanthoides* MACKAUER, 1961.
 † *P. fossilis* (MACKAUER, 1960) (Haut-Rhin, potassium layers, Tertiary-Oligocene).
 Genus: † *Promonoctonia* STARÝ (in litt.).
 † *P. quievreuxi* (QUILIS, 1940) (Haut-Rhin, potassium layers, Tertiary-Oligocene).
 Genus: † *Palaeoxys* MACKAUER, 1961.
 † *P. fuscus* (QUILIS, 1940) (Haut-Rhin, potassium layers, Tertiary-Oligocene).
 † *P. primigenius* (QUILIS, 1940) (Haut-Rhin, potassium layers, Tertiary-Oligocene).
 Species of uncertain generic position:
 † *Aphidius maximus* THEOBALD, 1937.

KEY TO THE FOSSIL GENERA

- 1 Three radial cells developed, separated from each other 2
- Wing venation reduced 3
- 2 (1) Pterostigmal cell complete. Antennae 11-segmented.
Ephedrus HALIDAY, 1833.
- Pterostigmal cell incomplete. Antennae at least 13-segmented.
† *Protephedrus* QUILIS, 1940.
- 3 (1) Interradial veins missing, radial cell 1 and median cell separated 4
- Wing venation with other characters 5
- 4 (3) First abscissa of radial vein fully developed. Antennae 30-segmented.
† *Propraon* BRUES, 1933.
- Antennae 18-segmented
† *Archipraon* STARÝ (in litt.).
- 5 (3) Pterostigmal cell distinctly complete 6
- Pterostigmal cell distinctly incomplete, although radial vein sometimes very long 8
- 6 (5) Ovipositor sheaths curved downwards, claw-shaped.
† *Promonoctonia* STARÝ (in litt.).
- Ovipositor sheaths slightly curved upwards 7
- 7 (6) Propodeum more or less areolated. Median vein not reaching wing margin
† *Pracaphidius* STARÝ (in litt.).
- Propodeum smooth. Median vein reaching wing margin.
† *Holocnismus* QUILIS, 1940.
- 8 (5) Radial and median cells confluent, separated by interradsial vein on their external side and by median vein on the lower side.
† *Pseudaphidius* STARÝ (in litt.).
- Radial and median cells absent 9
- 9 (8) Ovipositor sheaths slightly curved downwards, narrowed to the apex.
† *Protacanthoides* MACKAUER, 1961.
- Ovipositor sheaths slightly curved upwards. 10
- 10 (9) Propodeum smooth. Abdomen lanceolate. Tergite 1 triangular or much longer than width. 11
- Propodeum more or less carinated. Abdomen puriform, stout and short. Tergite 1 subquadrate. Appearance robust.
† *Oligoaphidius* QUILIS, 1940.

11 (10) Tergite I three times as long as wide.

† *Protodiaeretiella* STARÝ (in litt.).

– Tergite I triangular.

† *Palaeoxys* MACKAUER, 1961.

COMPARISON OF FOSSIL AND RECENT FAUNA. As no other fossil aphidiids are known up to the present day except for the Oligocene period, we can compare only the Oligocene fauna with the recent one. Nevertheless, the features of geographic distribution were found to be also helpful—we know that some districts of the Far East have little changed since the Late Tertiary; naturally, we cannot classify the species that occur now in the territory mentioned as 'living fossils' as they have developed since Late Tertiary as well (Their development is apparent from the comparison of the European and Far Eastern fauna which had no doubt a common origin before the area was broken in the Quaternary). However, the main features (generic) allow us to form at least a rough idea of the life conditions and generic composition of the Late Tertiary fauna.

As to the Oligocene fossils, we can only compare the differences in morphology, eventually their occurrence in certain floristic zones of the corresponding period.

The shape of tergite I was apparently mostly short and wide in the fossils, being mostly slender and comparatively long in recent forms. Thus apparently was an adaptation to the parasitism on aphids, nevertheless, the progressive tendency seems to be in the narrowing and lengthening of the tergite. This feature might result in a better adaptation to attack on aphids.

The number of antennal segments was mostly small in the fossils, being about 15 on the average. The recent fauna seems to have more, 20 and sometimes still more segmented antennae in some genera. In the recent fauna, too, the segments are mostly longer and narrow. Nevertheless, the number of antennal segments does not seem to be too useful a character for comparing fossil and recent faunas, the separate species of individual genera often exhibiting low to a high number of segments; in other genera, the number of antennal segments is generally higher, being low again in the others. The only single apparently ancient character as to the number of antennal segments seems to occur in the recent fauna in *Ephedrus* species, where there is a low (11) and in both sexes an equal number of antennal segments. As this genus is known from the Oligocene as well, the ancient type of this character seems to be well justified.

The structure of the propodeum. It was apparently often smooth, the areolation or carinae being comparatively rare. In the recent species, the propodeum is either smooth or bears a distinct areolation, which is often of generic or subgeneric value. This feature is somewhat surprising, as one would expect that the carinae would be present mostly just in the fossils, the reduction of such structures being then found in the recent forms. There is, however, no doubt that the fossil fauna has not been known completely from the Oligocene, so that the establishing of the generic relationship may not be possible in all cases.

Wing venation. In the fossils, the long radial vein and almost complete pterostigmal cell, and the median vein often reaching the wing margin, are a common character; otherwise the reduction of venation was apparently of a similar type as that of the recent genera—the *Ephedrus*-type being apparently the most ancient type as well. The recent forms are mostly characterized by the reduction of radial and median vein, the exceptions being rare and representing mostly isolated groups. The *Ephedrus*-type venation has been known both in the fossil and recent forms.

Ovipositor sheaths. The known fossils do not exhibit any special morphological

modifications of the sheaths: they are mostly narrow and long, curved slightly upwards, slightly narrowing to the apex or claw shaped. This feature of the fossils seems to be a character of relatively poor adaptation to aphids, due just to the obvious morphological uniformity. The recent forms, on the contrary, both in separate genera, or sometimes in species of the separate genera, often exhibit quite a number of adaptations as to the shape of ovipositor sheaths, accessory prongs being developed in certain cases as well.

When comparing the known fossil fauna and recent faunas, we can summarize the results as follows: The fossil (Oligocene) fauna of aphidiids is characterized by mostly a low number of antennal segments, broad and short tergite 1 and more or less complete pterostigmal cell. The generic composition of the fossil aphidiids is rather different from that of the recent fauna, although in a number of cases both fossil and recent genera seem to exhibit a certain relationship. Rarely, the same genus has been known to occur since the Tertiary-Oligocene up to the present day.

The classification of the recent fauna of the Far East, which is believed to resemble closely the Late Tertiary fauna that was distributed at almost the very same area at that time, has shown that the generic composition of the Late Tertiary fauna was obviously very similar to that of the present day. The Quaternary period, therefore, does not seem to cause any deep changes in the generic composition of the aphidiids.

MAIN DIRECTIONS. There is no doubt that the fossil fauna of the aphidiids is too poor and restricted as to its occurrence in time (Oligocene only) to base certain phylogenetical conclusions on it. In the absence of fossils it is necessary to evaluate certain features of the recent fauna with respect to the classification of the evolution of the group. On the one hand, geographic distribution of the group may be useful, on the other hand, the relations to the host group—the presence of which in a certain community is naturally a necessary factor of parasite occurrence—might be helpful for such a task.

— *Geographic distribution criteria.* Paleobotanical data have shown (MARKOV, 1951) that the main change in the plant kingdom, since the end of the Cretaceous, is the differentiation of plant cover to separate zones and provinces. As we have found that the recent fauna of the aphidiids is attached to certain types of floristic zones, we can suppose that similar types were favourable for the ancestors of the aphidiids in the past periods as well. For this reason, the origin of the main types of the present day flora (after MARKOV, 1951) must be mentioned to enable the derivation of the original floristic zones in which the aphidiids have developed since the older times.

1. Forest of the tropical belt. The forest flora of a tropical belt of today seems to have changed least. The tropical zone, however, has been influenced through climatic changes—similarly as the whole earth—since the beginning of the Upper Cretaceous. These changes, however, have not such a decisive influence on the plant cover as in the great latitudes. According to VULF (1944) the tropical floras can be classified as Tertiary floras which have survived up to the present day. Of the tropical forests, the evergreen forests of the moist tropics seem to exhibit the best archaic character—such a number and quantity of species may not be found in other floras anywhere on the earth. Naturally, although exhibiting such features, these floras have been in continuous development.

Therefore, the tropical forest exhibits the features of relative constancy as to its origin. Were the tropical forest a favourable zone for the parasites, one would expect that, on the one hand, the archaic forms of the parasites would occur here, on the other hand, the parasites would be rather common. Nevertheless, nothing of this is true: with the exception of some specialized groups, and widely distributed

species, too, the aphidiids as a group do not seem to occur in the moist tropical forest. The same is true as to their hosts—the aphids. Thus we may classify the tropical forest as not favourable for parasites both in the past and present.

2. Forest of the temperate (and subtropical) belt. The forest of this type was more distributed in the Upper Cretaceous and in the Tertiary than at present. It originally covered the territory of recent steppes of temperate latitudes and extensive areas in the Arctic, it had, however, another character.

The recent forest belt of the mild climate is formed by the zone of taiga and the zone of mixed forests. The taiga is characterized by the prevalence of coniferous forests with a certain percentage of deciduous trees (*Populus tremula*, *Betula*, etc.), and an extensive quantity of moors. The palearctic mixed forest zone is separated today into two great parts—European and Far Eastern (detailed development of this flora, see: History of the flora).

Forests of the temperate type are rather favourable for the aphidiids, which are rather common there. As to the origin of forests, certain forests of the temperate type have apparently represented favourable environment both for the aphids and parasites.

This conclusion was justified by the classification of aphid development too (SHAPOSHNIKOV, 1953, etc.). The most ancient groups of recent aphids are connected with trees, conifers, Fagaceae, Salicaceae, Ulmaceae, etc. Similarly, there are also many species distributed in the forest zone, while they are absent in the steppe and desert zone, where many species of younger aphid groups connected with herbs can merely be found. Moreover, there are many aphid species absent in the forest zone, whose biology is connected with grasses, similarly to some root aphids, etc. And finally, xerophilous aphid forms are totally absent in the forest zone.

All this can be applied generally also to parasites. In the forest, too, we can find some parasite groups that are closely attached to the ancient aphid groups (Pemphigidae, Lachnidae, Chaitophoridae, etc.) and do not attack other aphid groups either. This relative constancy of relationship can be of very ancient character, showing the evolutionary isolation of such groups.

3. Steppe and desert flora. The xerophytization process in ancient floras can be recognized since the end of the Paleozoic. Nevertheless, the original feature of recent deserts of subtropical and temperate zones may be found only from the Upper Cretaceous. In this period, too, the desert type of landscape of C. Asia originated. The xerophytization of plant cover gradually reached greater importance during the Tertiary. It spread from the lowland of the temperate zone of Asia to the lowland landscape of southern Europe, where steppes originate in areas formerly covered by forests. The Tertiary period is the period of development and spread of steppe and deserts in the lowlands of the temperate zone of Eurasia. As to the taxonomy, it is necessary to stress the fact that the steppe flora is represented mostly by various grasses, the development of the group being typical just for the Tertiary and Quaternary, due to the extensive steppe districts, although the ancient grasses were originally plants of the tropical forest. Because of the xerophytization and cooling of the climate, grasses were the most suitable plants for such conditions, having a great preponderance when compared with the forest.

Therefore, the steppe zone is without any doubt much younger than the forest communities of corresponding periods. In the recent period, the aphidiids are rather numerous both quantitatively and qualitatively in this zone. The most widely specialized species of parasites may just be found in the steppe zone, besides other less or strictly specialized species. Moreover, the steppe species never occur in forest habitats.

4. The tundra zone is the youngest floristic zone. Its development was at the end of the Tertiary and at the beginning of the Quaternary, possibly only in the Quaternary.

The aphidiids are known only from the forest tundra zone of today, being represented by species which are distributed also in the temperate forest zone, although being developmentally connected and preferring the boreal communities. This group of parasites is associated through aphids with such plants as *Betula*, *Salix*, *Populus*, so that their contemporary occurrence in this association is well understandable. There is no doubt that they are less in number of species and represent a developmental trend of less importance, possibly an extreme adaptation of parasites to cool climatic conditions.

We can conclude the aforesaid in such a way that the zone of temperate forests and zone of steppes exhibit the richest fauna of parasites. Of these, the temperate forest zone is more ancient, being apparently the original zone where the parasites have developed and spread to the steppe zone.

Summarizing, the geographic distribution of the recent fauna of aphidiids may be well characterized as follows: In their north-south distribution the parasites are connected with separate floristic zones. The tundra zone seems to be inhabited secondarily by the fauna of forests (boreal type). In the taiga (coniferous forest) zone numerous aphidiids occur, being a strictly specialized group that differs both generically and by their host specificity from the other fauna of the Aphidiidae. The fauna of deciduous forests is very rich, including the greatest part of the recent genera, the number of species being high as well, the host specificity range of the parasites is various, both ancient to young aphid groups being parasitized. Steppe fauna has a very similar generic composition as the deciduous forest fauna; the number of species is very high. Semi-desert and desert zone seems to be inhabited in a lesser degree by the aphidiids. The tropical forest (some parts) belt is inhabited by smaller and specialized groups of aphidiids, which are connected with corresponding specialized groups of aphids in addition. Widely distributed or cosmopolitan species are not mentioned as they obscure the dependence mentioned.

Thus, the geographic distribution of the recent aphidiids clearly shows that the greatest part of species is connected with the temperate-subtropical climate belt, inhabiting mainly deciduous forest and steppe type habitats. Coniferous forests of the temperate-subtropical belt are inhabited by relatively numerous but specialized parasite fauna, which has no apparent relation to the other groups. Similarly, the tropical forest is characterized by relatively poor and strictly specialized parasite fauna, which is attached to tropical aphid groups.

— *Taxonomic criteria.* 1. Generic composition in the separate floristic zones. Although the generic composition of the aphidiids of today does not seem to be too helpful as to the evaluation of host specificity of parasites, some records may be used at least for the separation of certain groups. The comparison of the generic composition of the aphidiid parasites of separate zones has shown that some differences can be found here as well. A coniferous forest is characterized by a separate fauna of parasites, which is rather peculiar and has no apparent connection with other aphidiids. It is interesting, too, that the more ancient forms as to wing-venation, etc., can be found in the deciduous forest, while the parasites of the Lachnidae exhibit apparently less ancient characteristics. Nevertheless, both their general morphology, host specificity, occurrence in coniferous zone, etc., seem to show distinctly their different character as to their recent relations, and to their origin perhaps as well. Other criteria must be used, such as embryology, anatomy, etc., to ascertain their true position. For the present, they seem to have developed from other ancestor groups which seem really unrelated

to the ancestors of other recent aphidiid groups. The peculiarities of the recent coniferous forest parasite fauna may be observed both as to the genera and species; some exceptions known are undoubtedly of secondary character and the relations may be easily derived. All the parasite inhabitants which are typical of a coniferous forest, attack exclusively the Lachnidae. A tropical rain forest seems to exhibit similar features, although they are somewhat less apparent, or rather, less known. The parasites may or may not be partly found to have a certain relationship to other genera, nevertheless, their occurrence in habitats is inseparable from the occurrence of the Greenideid host aphids as well. The generic composition of parasites occurring in the deciduous forest zone and the steppes is practically identical; however, certain genera, usually less numerous in number of species, and apparently either archaic or too young, may be found in each zone. The generic resemblance with respect to the history of floras, recent distribution of parasites, etc., seem to clearly prove the derivative position of the steppe fauna. Nevertheless, each fauna has developed in a separate way, the species being mostly strictly separated today (relative stenotopy).

2. Developmental trends and the genera. We have stated on the base of various criteria that the main developmental trend of the aphidiids was 'deciduous forest-steppe' trend, while less important trends were in the coniferous forest and tropical rain forest. Generic composition mentioned above may really support such an opinion. Genera of the aphidiids associated with a coniferous zone have no relationship—taxonomic, ecological, or zonal—to other groups of the Aphidiidae; they occur in a coniferous forest zone exclusively, having no connection with the steppe—the latter fact is rather important. On the contrary, the genera represented in a deciduous forest zone are in the previous number of cases represented in the steppe zone too; this means that a certain part of species has gradually spread and further developed in the steppe zone, the progressive trend of the group 'deciduous forest-steppe' being thus represented in the progressive genera also.

—*Host specificity criteria.* 1. Possible adaptation of the ancestors to parasitism. First known fossils of aphids are known from the Perm period (see: BEKKER-MIGDISOVA, *rfc.*). Fossils from the Upper Jurassic period (BEKKER-MIGDISOVA, 1966), the family Genaphididae, exhibit almost all the plesiomorph characters as to the body and wing venation, which are typical of the present representatives of the related aphid groups, some ancient characters being found in the venation only. The recent relatives belong to the families Lachnidae, Callaphididae, Aphididae. Fossil aphids are not rare in the Tertiary either. HANDLIRSCH (1925) records 17 extinct genera and 5 surviving ones (*Chermes*, *Aphis*, *Schizoneura*, *Lachnus*, *Pemphigus*), 56 species altogether, from all over the world (12 species from the Balic Amber, 23 from the Miocene of Florissant, 2 Oligocene—British Columbia, etc.).

This means, with respect to the development of the host and parasite relations, that not later than in the Upper Jurassic period can we find almost the same features of host body morphology as in the recent period. At the Upper Jurassic period, apparently, the ancestors of the Adelgoid group were distinctly separated. Therefore, as the above mentioned fossil aphids possess the characters to which the recent parasite groups are so well adapted, we can conclude that there might have been also some parasite groups occurring in the Upper Jurassic period, which were specialized on the 'aphidoid' type of aphids. Since that time at least, the parasites theoretically had the possibility to adapt themselves to parasitism on aphids.

2. Host specificity in fossils. Unfortunately, this feature of biology of the fossil aphidiids cannot be ascertained today. We can obtain some information from the composition of the fossil fauna of aphids, the nature and composition of fossil flora, etc. Nevertheless, all the derivation, except maybe the Late Tertiary from which

some parts of the fauna have partly survived up to the present day, might be influenced by our recent knowledge of the parasite host specificity which might just have been of a different type in ancient times.

3. Phylogenetic age of the hosts. As has been mentioned in the aphid-host plants relationship, the phylogenetic age of the host plants mostly does not influence the host specificity of aphids, phylogenetic parallelism being relatively rare (in Rosaceae, etc.). The same applies to the parasites. Except for some isolated groups, such as the Lachnidae, Greenideidae, etc., the parasites cover different aphid groups, irrespective of their phylogenetic age. Naturally, there may often be distinguished some groups of parasite species that are more or less adapted to certain aphid groups in a given type of habitat, or, in extreme cases, a certain number of more or less strictly specialized parasite species can be found as well. The mentioned features may be recognized from the host range of different parasite species of most of the aphidiid genera, both phylogenetically older and younger ones: *Ephedrus*, *Praon*, *Aphidius*, *Lysiphlebus*, *Monoctonus*, *Trioxys*, and others; in genera more numerous as to the number of species, this feature is more apparent.

4. Floristic zones.

A. Seasonal history of aphids. As we have mentioned earlier (see: Seasonal history), the seasonal history of aphids changes in dependence on latitude. While in certain districts a complete life cycle takes place (except for secondary changes due to the influence of the Quaternary, etc.), only parthenogenetic reproduction occurs in the same species in the south.

B. Aphid responses to drier climate, adaptation of parasites. A certain part of aphids has responded to drier climatic conditions by development of obligatory migration or arrested states in development. Both these phenomena have clearly an adaptive sense, which can be seen from their development in various groups of aphids as well as from their seasonal history-dependence on various climates.

These adaptations of host aphids, resulting in their seasonal lack (either entirely or the presence of unsuitable stages for parasitization only), have naturally caused certain changes in parasites host specificity. On the one hand, the parasites developed corresponding seasonally dependent arrested states of development, with a re-appearance at the period when the aphid is again present in the habitat; on the other hand, they have enlarged their host range which resulted in their ability to parasitize a number of aphid groups so that the parasite was able to occur in a given type of habitat throughout the whole season.

C. Invasion of aphids and parasites to new habitats. In the temperate deciduous forest and steppe zones (Europe), the following groups of aphids approximately can be recognized, if their adaptation to drier climatic conditions are used as the criterion.

I. Deciduous forest

(a) constant deciduous forest species. They are adapted to forest environment, being both phylogenetically old and young. Usually holocyclic monoecious species (in some cases, the arrested states in development may cause the absence of stages suitable for parasites, although the aphids are present in the habitat).

(b) Temporary deciduous forest species. There are the holocyclic dioecious species, their obligatory migrations being of 'forest-steppe-forest' type. They are adapted both to the forest and steppe environment. Adaptations to drier conditions resulted in their seasonal occurrence in steppe habitats, nevertheless, their developmental dependence on the forest environment is deep, so that they still spend a certain part of their seasonal history in forest environment as its typical inhabitants. Just in this group, this feature is rather remarkable, if the aphids are also distributed in the south and occur in steppe habitats exclusively as parthenogenetic progeny.

II. Intermediary zone

A number of aphid species can be found in the intermediary zone, being nevertheless dependent on the presence of their host plants, both primary or secondary.

III. Steppe (cultivated steppe)

(a) Constant steppe species. They occur here all the year round.

(b) Temporary steppe species. These are the dioecious species, which spend a certain part of their seasonal history in the steppe, although they are still connected with the forest in their biology.

The parasites, naturally, have been unable to develop a similar seasonal obligatory migration as the aphids. They are basically habitat dependent, and in this respect they can be divided as follows:

I. Deciduous forest

(a) Specialized parasites of some old aphid groups, such as the Callaphididae, which have no relation to other aphids.

(b) More widely specialized species, covering both dioecious and monoecious aphids in their host range.

(c) Specialized parasites of dioecious aphids. (They respond to seasonal host absence by seasonal arrested states in development).

(d) Specialized parasites of younger aphid groups which do not attack dioecious aphids.

II. Intermediary zone

In this zone, there occur some parasites which are less habitat dependent, usually occurring both on the edges of forest and steppe. They represent apparently the trend or route in parasite development showing how the group, i.e. its part, might gradually invade steppe habitats.

III. Steppe (cultivated steppe)

(a) Specialized parasites of steppe aphid species, which are phylogenetically older; they do not attack other aphids.

(b) More widely specialized parasites, covering both steppe species and dioecious aphids that occur seasonally in steppe habitats.

(c) Specialized parasites of younger aphid groups, which do not attack other aphids, either dioecious or phylogenetically older ones.

Therefore, there is a basic difference recognizable between the aphids and parasites as to their invasion of new habitats (from deciduous forest to steppe), when their present distribution and habitat dependence are used as a criterion.

In the aphids, besides the constant species which are connected with a given environment throughout the year, there are species which obligatorily change the kind of habitat, being present in a given type of habitat only seasonally. The parasites, on the contrary, are primarily habitat dependent, no seasonal occurrence in different types of habitats being typical for them. The latter phenomenon is clearly recognizable from peculiarities in their biology. As to the development of the group, it is apparent that the adaptation to aphid obligatory migrations is successive and secondary in the parasites, showing the primary strict habitat dependence of this group as well as the importance of spread to new habitats as a factor in the phylogeny of the group.

5. Natural groups of aphids. As the separation of the aphidid parasite group from the related ancestors of the present Braconidae is apparently of a very old date, it is difficult to establish the original group of aphids, which the ancestors of the recent aphid parasites had attacked. The comparison of the host range of the Aphidiidae as a group has nevertheless clearly shown that the parasitism of aphids began not earlier than two main aphid groups—the adelgoid and the aphidoid—had separated from each other. This statement seems to be well justified by the fact that the present

fauna of aphidid parasites does not include any parasites of the Adelgoid aphids. As to the other natural groups of aphids and their aphidiid parasites of today, their relationship is characterized—with the exception of some groups—by the parasitization of members of various parasite genera on various natural groups of aphids irrespective of their phylogenetical age, various degree in parasite species dependence on taxonomy and ecology of their hosts being recognizable (see: Host specificity).

6. Role of the mode of aphid life. With respect to their occurrence in various types of habitats and the development of their relations to their hosts, the plants, the aphids have developed and adapted morpho-ecologically in various ways (partly see below). These aphid adaptations may be either seasonal (gall aphids, etc.), or they may be continuous, if the aphid life cycle occurs in more or less the same environmental conditions throughout the whole season. These responses of aphids to the environmental conditions have naturally caused corresponding adaptations in the parasite group. For this reason, we may well recognize more or less specialized groups among the parasites, either morphologically or ecologically, to various ecological groups of aphids. Generally, the ecology of the host, its morpho-ecological type, is one of the basic factors influencing the host range of the parasites, the taxonomical affinities having a various degree of importance as well (see: Host specificity).

7. Role of aphid morphology. As we have mentioned earlier, the adelgoid type of aphids apparently was quite left aside by the parasites. Neither the old nor any of the younger parasite groups (secondary adaptation) is known to parasitize the adelgoid aphids.

As to the 'aphidoid' type of aphids, these aphids are the group to which the parasites have fully adapted themselves. In case that a too peculiar morphological type had developed in such aphids, it can be neglected by the parasites as well, for example the aphid family Thelaxidae and its aphidiid parasites. The Thelaxid aphids exhibit a somewhat 'coccidoid' morphology in a various degree. We know aphidiid parasites of the *Thelaxes* sp. (Europe), but the *Cerataphis* species are obviously disregarded by the parasites due just to their coccidoid shape of the body. This resemblance is stressed by the parasitization of *Cerataphis* species by the chalcid flies (*Encarsia*, etc.), which attack hosts as the Aleurodids, coccids, etc. mainly.

However, there is known a certain number of aphid species that exhibit typically 'aphidoid' features, but we do not know any aphidiid parasites attacking them, although numerous samples were reared by various authors. Although this group of aphids is not numerous, we still have no explanation of this peculiarity in parasite host specificity (*Lachnus roboris*, *Callaphis juglandis*, etc., see Relations of host-parasite groups).

8. Host range. Host specificity range cannot be classified in an isolated way, but in a complex manner. Mainly, it has to be classified with respect to the given floristic zone, which generally determines the main trend of the aphidids.

From this standpoint, the coniferous forest inhabiting parasites have to be classified as a branch of the general trend, which can include both progressive and regressive species, nevertheless, its development does not correspond to the general trend.

The trend of deciduous forest inhabiting parasites is generally progressive. Nevertheless, a further subdivision can be made similarly to the above mentioned division of parasites in deciduous forest and steppe zones in Europe. A wide host range, covering both the younger groups of dioecious and monoecious aphid species seems to be the most progressive adaptation.

A similar situation may be found in the steppe. Here, too, a wide host range seems to be progressive, in case that phylogenetically young aphid groups are covered, being constant or temporary members of the steppe community.

Therefore, we have to distinguish between the host range of the aphidiids as a group, and host range of different genera and species. Generally, a wider host range seems to be progressive (for details, see Host specificity).

— *Fossils* and related records on climate, flora, etc., can help us to get an idea about the composition and occurrence of aphidiids in a certain district in a given period. Nevertheless, care must be taken in order not to make some mistakes, the following being mentioned:

1. Fossils usually represent samples from a restricted area. They can hardly represent a full composition of the fauna occurring in the given period, which depends on the quantity of fossil specimens obtainable. Although there are records showing that fossil floras were more uniform than the present ones, this factor must be kept in mind. The Baltic amber specimens for example are rather useful usually being well preserved and easily determinable. Nevertheless, they represent examples of forest fauna of a certain type, which occurred in the Early Oligocene (or Late Eocene) in a given area, under a warm to subtropical humid climate. They give no idea of the faunas of other types, so that—such fossil species not being known—we cannot classify the relations of separate faunas. The relative significance of fossils could be illustrated by collecting some aphidiids in a subtropical forest in sticky traps and relating their classification to other fauna known.

2. The fossils cannot be discussed in terms of present-day zoogeographical regions.

This phenomenon is well understandable from the comparison of the history of the floras with their present distribution. Great migrations of floras occurred in the past with corresponding changes in the composition of fauna (see: Geographic distribution).

For example, aphids of the family Greenideidae, which is distributed today in south-eastern Asia, were present in the Miocene on the territory of present day Europe (SHAPOSHNIKOV, 1953) this being naturally in agreement with the distribution of corresponding floras of that time. Apparently, the parasites, which are represented by a strictly specialized group today, were probably also present in this area. Nevertheless, further changes in climate and successive changes in flora caused the extinction of the Greenideidae in Europe and their restriction to the territory of the present day south-eastern Asia.

Generally, fossil specimens, though poorly known, give us a rough idea of the character of the fauna (or its part) of the given period.

Oligocene specimens (Haut-Rhin, France) described by QUILLIS (1940) have enabled the comparison of the fauna of the given period, and differences were found to show the distinctness of the fauna from the present one, as well as the characters that were typical of fossil faunas with respect to the comparison with the present fauna. Similarly, Amber records are valuable. The general research of climate and floras has shown (see: CROWSON, 1965) that similar conditions apparently exist today in south-eastern Asia, where also living species of genera represented in the Baltic Amber often occur; however, in critically revised groups of insects about half of the genera in the Amber are extinct. In the case of aphidiids, the comparison of Far Eastern fauna of today enables us to get a rough idea about the probable composition (generic) of the fauna of the subtropical forest of the early Oligocene.

— *Conclusive notes.* Summarizing, we can conclude that the main trend of evolution of aphidiid parasites corresponds to the main trend of their hosts—the aphids.

In the aphids (SHAPOSHNIKOV 1959) the main trend of evolution is connected with their transition from conifers to hardwood trees, from trees to shrubs, from trees and shrubs to herbs, with no dependence on the phylogenetic relationship and age. This is in agreement with the general phylogenetical direction of plants, the cause being

identical—adaptation to the occurrence in conditions of a drier climate.

Nevertheless, just as in the aphids and their relation to plants, parallel-evolution may be observed in a relatively low number of cases, while the adaptations of ecological character have apparently played the main role in the development, the parasite responses to environmental conditions often bearing specific features, different from those of their hosts—the aphids.

MAIN FACTORS. All the factors mentioned below must be understood as part of a unique complex, the members of which play a different degree of role in various periods of the phylogeny of the group; the influence of some of them seems to be relatively immediate, others may seem rather distant as to their significance, which, however, may be substantial. Many other features might naturally be mentioned, but there would be much theoretical combination with respect to the level of the recent state of research.

To understand the main factors that inhibited the adaptation of a certain group of the parasitic Hymenoptera to parasitism on aphids, we should mention briefly the general trend of the whole order of Hymenoptera. Basically, the ancestors and ancient groups of the Hymenoptera belong to the phytophagous species. The main developmental trend—besides the phytophagous one—was the adaptation to parasitism and predatory life, some other groups, however, developed in a very specialized way (pollinators, social insects, etc.).

The developmental trend of the parasitic Hymenoptera seems—due to the host specificity of the whole group—to be directed as to cover other insects, and in a lesser degree other arthropods as well, by parasitism or predation mostly in the larval stage of development. Various groups of parasites have developed in consequence. Aphids represented apparently a group of insects that was not covered during the past periods by any other parasites that would compete successfully with the Hymenoptera, so that one of the group of the Ichneumonoid complex adapted to aphid parasitism. It has been obviously successful as this adaptation has gradually resulted in strict parasitism and adaptation of this group—the aphidiids, i.e. their ancestors—to the aphids.

Climatic changes have played the main role (see: Phytogeographic principles) in the development of plant formation. As we have mentioned earlier, aphids represent a group that has apparently become adapted in the best way and developed in temperate to subtropical conditions, which have been connected with the climatic changes since the Late Cretaceous. The drier climate has caused deep changes in the original homogeneity of the flora, separate zones having originated. With respect to the development of the separate floristic zones we can conclude that the deciduous forests of milder climatic zones were apparently the best environments for the development of aphids and their parasites as well, a further developmental trend being in adaptation to steppe conditions. Besides, coniferous forests in milder climates and in a lesser degree tropical rain forests were invaded by specialized groups both of aphids and parasites.

The data obtained from geographic distribution, host range, fossils, etc., enable the elaboration of a principal conclusion, that the aphidid fauna of the Late Tertiary to the beginning of the Quaternary is generically very similar to the present one. Glaciation and other changes in the Quaternary, and successive disjunction of floristic zones, had corresponding effects in parasite areals as well. Some of the populations have developed as a separate species, some of them remained obviously unchanged. In every case, the Quaternary, on the one hand, has caused the suppression of the fauna in certain districts, on the other hand, it has stimulated the origin and

development of new species. The ability of the aphidiids to reach the existing number of species and cover the present area of distribution seems to be proof of the evolutionary progressive character of the group.

Floristic zone-dependence of the parasites is basical as to their occurrence. The aphid migration, which has been originally stimulated by the adaptation to the conditions of a drier climate, is simultaneously connected with the seasonal transition of aphids to other types of habitats; nevertheless, the original connection of such species with forest habitats still occurs. On the other hand, some groups have gradually spread to steppe habitats and they occur there exclusively, their original dependence of the forest being completely lost. The parasites, naturally, were forced to adapt themselves to new environmental conditions as well. But, they have been more stenotopic and they responded to the changes of environment in a somewhat different way than the aphids. A part of the deciduous forest fauna apparently gradually invaded the steppe habitats, this being apparent in a certain part of the recent aphidiids as well and they gradually also broke the contact with the forest altogether. For this reason, there is today a strictly differentiated fauna of the forest and steppe habitats, the intermediary forms occurring in a lesser degree. The generic composition, however, which is roughly the same both in the deciduous forest and in the steppe zone, shows the apparent relationship of the dependence of the steppe fauna on the deciduous forest fauna as to the origin of the former.

PROGRESSIVE OR A REGRESSIVE GROUP? Before the classification of the parasites as a progressive or a regressive group is dealt with, it is necessary to mention some brief notes on the whole food chain 'plant—aphid—aphid parasite' in a community in the broadest sense.

The plants are generally classified as a group that has been deeply influenced by the Quaternary, it is, however, in a state of recreation, and has become deeply progressive in evolution. This opinion is stressed generally by botanists (see Rfcs. on Phytogeography), the evolution of many groups and appearance of new forms being mentioned as one of the proofs. Naturally in the frame of community equilibrium level, the group in evolution causes the appearance and adaptation of parasitic organisms. This is true of the plant parasites, the aphids, too. The aphids, being temperate in origin, were naturally deeply influenced by the changes of their host plants both due to drier and cooler climatic conditions. Although these were in a corresponding way deeply influenced by the Quaternary, the number of species and the adaptation of aphids to new conditions that have later appeared means that they are a progressive group as well. There is no doubt and this is true of their host plants also, both progressive and regressive groups may be recognized among the aphids; as the progressive groups we can apparently classify such groups the biological features of which correspond to the general trend of aphid evolution. Therefore, we must distinguish between the development of the aphid group as a whole and the development of separate aphid groups. Similarly, the aphids seem to be a progressive group in certain climates only (temperate-subtropics), while tropics are mostly inhabited by other homopterous insects, which seem to be better adapted to such conditions.

What has been said about the plant-aphid relationship applies to the aphid parasites: In the frame of community equilibrium level, the aphids needed to be limited by their own enemies—the aphidiid parasite group has apparently adapted in consequence.

As both the plants and aphids represent progressive groups, the same appears to be true of the aphidiid parasites. They, too, are best adapted to a temperate-subtropical

climate. The research of aphid parasites has shown that there are practically no other aphid parasites that could successfully compete with the aphidiid parasites as a group. The chalcid parasites, which may sometimes compete, are mainly concentrated to parasitism on other groups, their significance being important in a relatively small number of cases.

A careful classification of the host range of separate parasite species has shown that there are various groups of parasites which are more or less attached to various groups of aphids. In the greatest part of genera we can find strictly specialized to widely specialized species. Similarly, taxonomy and ecology of aphids play various roles in the host specificity of parasites. Although the taxonomical host-parasite affinities may be applied in some cases only, their application in case of ancient aphid groups in connection with corresponding habitats is very useful in recognizing the basic schemes of parasite evolution as to its general trend. Although there are certain differences between the adaptation of aphids and parasites to the conditions of the environment, there is no doubt that the main trend of parasite evolution corresponds to the main developmental trend of aphids—i.e. adaptations to the conditions of a drier climate.

Summarizing, the aphidiid parasites may be classified as a progressive group of aphid parasites.

NATURAL SYSTEM. When the level of our knowledge of the fauna of the Aphididae of the world, their ecology, ontogeny, as well as the knowledge of the fossil faunas, is compared, the elaboration of a natural system of the Aphidiidae seems still to be unjustified. Some attempts are known from the literature of the present day (MACKAUER 1961, 1963, 1965, etc.), nevertheless, the mentioned systems may be classified as rather artificial and do not correspond to the conditions that seem to occur in the group.

Our comparative studies have shown that there undoubtedly occur a number of natural groups among the Aphidiidae, nevertheless, the relationship of these groups as to rank and mutual connections is difficult to classify as the criteria that would be used are known on a very unequal level; every classification of the aphidiids, based on a separately taken character with no respect to the others results certainly in an artificial system. In applying different characters to aphidiids, several and rather different systems from each would be obtained. The complex application of the characters mentioned is necessary before any really useful scheme of the system of the aphidiid parasites can be elaborated. It is for this reason that the level of our knowledge of various characters as a whole is rather unequal, we consider any further subdivision of the Aphidiidae to be artificial, as almost every genus would need to be separated as a higher taxonomic unit.

— *Analysis of criteria.* The below mentioned criteria were used for the separation of the main natural groups of the Aphididae. The review of natural groups shows on the one hand the inequality of the knowledge of different criteria in various groups, on the other hand the fact that more or less natural groups are rather differentiated from each other. The phylogenetical relations are believed to be more distinct on the basis of further research of embryology, anatomy, etc., which has been very poor until now.

Embryology. Contemporary studies have shown, although very scarce, that the main phylogenetical relationship among the certain groups, which, however, seem to be rather differentiated today, might be shown on the basis of embryology. The shape of the eggs, blastogenesis and morphology of instar I larva seem to be rather important.

Bionomics. Rather important features and differences were found in the bionomics of separate aphidiid groups (mode of pupation, of emergence, etc.).

Morphology of adults. There is no doubt that it is rather important and helpful to show the relation of different groups. Nevertheless, in case of morphological criteria namely, it is necessary to stress the fact of the different importance of various characters in different groups (wing-venation, number of antennal segments, shape of ovipositor sheaths), which may be clearly of a convergent type.

Anatomy of adults. Important differences in the anatomy, of ovaria namely, were found in various groups of the aphidiids. This is believed to represent also one of the sources of possibilities of separating the archaic groups inside the whole family.

Morphology of last instar larvae. The characters found in the last instar larvae seem to exhibit rather convergent features, due apparently to the practically identical environments—the host aphid body. The system elaborated on the base of last instar larvae characters (larval head namely) (ČAPEK, manuscript of a paper on last instar larvae of the Braconidae s.lat.) seems to us to be the result of the mentioned convergence, it differs extremely from the classification of separate 'natural' groups separated on the basis of applying complex criteria.

Ecology. The relationship of the parasite to the environmental conditions is of the greatest importance. With respect to the rough knowledge of factors that influence the determination of the development of the groups we evaluate the host-parasite relations, the geographic distribution of the parasite, etc. of today and in a number of cases of the pest as well. Host specificity knowledge and factors that have influenced it seems to be most useful.

Geographic distribution. The classification of the present distribution of the aphidiids and its comparison with the history of the flora, the aphid hosts, etc., may be mentioned as having, commonly with the host specificity, the key-position in the research of the aphidiid phylogeny.

Fossils. Only fossil species from the Tertiary (Oligocene) layers are known from several localities. The comparison of that and the recent faunas shows apparently a rather important connection in certain cases. Unfortunately, only morphological criteria may be mostly used in fossil specimens, and sometimes the character of floristic formations, climate, etc., of the given periods may be also used.

— *Natural groups.* All the known genera of the Aphididae have been separated into several groups with corresponding notes on their relationship; the genera unsatisfactorily described having been excluded.

Group 1: *Ephedrus* HALIDAY

Embryology: Eggs prolongately oval. Blastogenesis by differentiation of blastomeres. Primitive characters in the embryonal development, with poor differences from the general trend of development. Instar I larva with comparatively long simple cauda and two perpendicular accessory prongs. Bionomics: Pupation inside mummified aphid. Mummified aphids black. Emergence hole on the apex of mummified aphid. Morphology of adults: Wing venation of *Ephedrus* type, almost complete in the frame of the family. Antennae with low number of segments (11), which is equal in both sexes. Notaulices developed. Propodeum areolated. Ovipositor sheaths prolonged, almost straight or slightly curved upwards, sparsely haired or pubescent. Abdomen lanceolate. Anatomy of adults: Ovaria divided into 3 long ovarioles, that are prolonged as far as the base of abdomen. Ecology: Occurrence in forest type, intermediary and steppe habitats. Host range: Various aphid groups, except the Lachnidae. Dependence on the mode of host life is various. Distribution: Mostly widely distributed species. Fossil relatives: The genus is known both from the Tertiary—Oligocene and present period. The most related genus

seems to be † *Protephedrus* that differs from *Ephedrus* in more reduced radial vein and higher number of antennal segments. Recent relatives: From recent genera, it seems to be most related to *Praon* as to embryology, shape of eggs, instar I larva and anatomy, differing, however, in wing venation, number of antennal segments, and some differences in bionomics. The phylogenetical connection of both the groups mentioned seems to be distinct.

Group 2: *Toxares* HALIDAY

Embryology: Unknown. Bionomics: Pupation inside mummified aphids. Emergence hole—position unknown. Morphology of adults: Wing venation complete (*Ephedrus* type)—Antennae with comparatively high number of segments, which is different in both sexes. Notaulices developed. Propodeum areolated, ovipositor sheaths triangular, trifid at extremity, curved downwards. Abdomen of ♀ rounded. Anatomy of adult: Unknown. Ecology: Occurrence in forest type and intermediary habitats. Host range: poorly known, probably some arboricolous groups of aphids except the Lachnidae. Distribution: Europe, Far East. Fossil relatives: Unknown. Present relatives: Unknown. The complete wing venation resembles *Ephedrus*, but the differences in other morphological criteria are too great (number of antennal segments, shape of abdomen, ovipositor sheaths, etc.).

Group 3: *Pseudephedrus* STARÝ

Embryology unknown. Bionomics: Pupation inside parasitized mummified aphid. Mummified aphids black. Emergence hole at the apex of mummified aphid. Morphology of adult: Wing venation with archaic and peculiar characters; pterostigmal cell almost complete, radial and median vein developed throughout, no closed radial and median cells. Antennae with low number of segments, different in both sexes (11—♀♀, 13—♂♂). Notaulices entirely absent. Propodeum areolated. Ovipositor sheaths almost straight, obtuse at apex. Abdomen of ♀ lanceolate. Anatomy of adults: Unknown. Ecology: Occurrence in forest type habitats (tropical cloud forest!). Host range: Parasites of certain primitive Callaphidid aphids (*Neolizerius* sp.). Distribution: Cuba, and probably some mountain parts of South America. Fossil relatives: Unknown. Present relatives: It seems to be an isolated group, with rather ancient characters in wing venation. It might have certain relations to *Ephedrus* due to the black colour of mummified aphids and the position of the emergence hole on the apex of aphid body.

Group 4: *Areopraon* MACKAUER, *Praon* HALIDAY, *Dyscritulus* HINCKS

Embryology: Eggs prolongately oval. Instar I larva with comparatively long simple cauda and two perpendicular accessory prongs. Bionomics: In probably more primitive genera (= *Areopraon*) pupation inside mummified aphid, in the others under parasitized aphid inside a separate cocoon, the empty aphid skin being mounted on the top of the cocoon (*Praon*, *Dyscritulus*). In more primitive genera (*Areopraon*) the emergence hole is on the apex of aphid body (pupation inside aphid skin), in the other genera (*Praon*, *Dyscritulus*) in lateral portions of their separately mounted cocoon. Morphology of adult: Wing venation of *Praon* type and more reduced. Antennae with low or higher number of segments, which is different in both sexes. Notaulices developed. Propodeum partially areolated to entirely smooth. Ovipositor sheaths slightly curved upwards, sparsely haired or pubescent. Abdomen of ♀ lanceolate. Anatomy of adult: Ovaria separated into 2 ovarioles, rather long, prolonged to the abdominal base. Ecology: Occurrence in forest type, intermediary and steppe habitats. Host range: Various aphid groups, except the Lachnidae (with a single exception of a secondary character) *Areopraon*—gall aphids, *Praon*—mostly freely living aphids, more or less specialized parasites. *Dyscritulus*—strictly specialized parasites of some freely living aphids. Distribution: Not too widely distributed

species, sometimes vicariant. Fossil relatives: † *Propraon* BRUES, † *Archipraon* STARÝ. The relationship with the fossil genera is rather close. Present relatives: According to morphological characters and bionomics it represents a very typical group. Developmental connections probably with group 1.

Group 5: *Pauesia* QUILLIS, *Xenostigmus* SMITH, *Metaphidius* STARÝ & SEDLAG, *Diaeretus* FÖRSTER

Embryology: Unknown. Bionomics: Pupation inside mummified aphid. Emergence hole in the dorsal portion of mummified aphid. Morphology of adult: Wing venation of *Pauesia* type and more reduced. Antennae with low or high number of segments, which is different in both sexes. Notaulices distinct anteriorly to being entirely effaced. Propodeum areolated. Ovipositor sheaths of various shape, mostly curved upwards (more rarely ovipositor slightly curved downwards (*Diaeretus*), sparsely haired. Abdomen of ♀ lanceolate, modifications and accessory prongs on abdomen rare (*Metaphidius*). Anatomy of adult: Unknown. Ecology: Occurrence in forest type and intermediary habitats. Host range: Specialized parasites of Lachnidae (Cinarine groups, with some exceptions). Distribution: Often widely distributed species. Fossil relatives: A specialized and strictly characterized group of parasites of the Lachnidae. It seems to be very isolated from the other groups of the family.

Group 6: *Protaphidius* ASHMEAD

Embryology: Unknown. Bionomics: Pupation inside mummified aphid. Emergence hole at the apex of mummified aphid. Morphology of adult: Wing venation of *Pauesia* type. Antennae with unusually high number of segments, which is different in both sexes. Notaulices more or less developed. Propodeum carinated. Abdomen of peculiar shape, sham-ovipositor developed. Anatomy of adult: Unsatisfactorily known. Ecology: Occurrence in forest habitats. Host range: Specialized parasites of Lachnidae (*Stomaphis*). Distribution: Europe, Far East. Fossil relatives: Unknown. Present relatives: It seems to be an isolated group of aphidids. Morphologically it mostly resembles *Pauesia* spp., in some characters, parasitizing a related host group, too.

Group 7: *Archaphidius* STARÝ & SCHLINGER

Embryology: Unknown. Bionomics: Pupation inside mummified aphid. Position of the emergence hole unknown. Morphology of adult: Wing venation of *Aditus* type. Antennae with higher number of segments, probably different in both sexes. Notaulices effaced. Propodeum partially carinated. Ovipositor sheaths curved upwards to straight. Abdomen of ♀ lanceolate. Anatomy of adult: Unknown. Ecology: Occurrence probably in forest type habitats. Host range: Specialized parasites of the Greenideidae. Distribution: Restricted to Far Eastern district, probably also in other parts of the Indo-Malayan (= Oriental) region. Because of the strict specialization restricted on the distribution area of the host aphids. Fossil relatives: † *Holocionus* QUILLIS—judging from certain morphological resemblances (wing-venation). Present relatives: Unknown. The similar venation as in *Aditus* is clearly of convergent value only. It seems to be an isolated and specialized group.

Group 8: *Aphidius* NEES, *Lysaphidius* SMITH, *Diaeretiella* STARÝ.

Embryology: Eggs lemon-shaped. Blastogenesis by delamination. Distinct adaptation to parasitism, distinct differences from the general direction of development, less palingenetic peculiarities. Instar I larva with simple caudal appendage. Bionomics: Pupation inside mummified aphid. Emergence hole in the dorsal portion of mummified aphid. Morphology of adult: Wing venation of *Aphidius* type and more reduced. Antennae with low or higher number of segments, which is different in both sexes. Ovipositor sheaths comparatively short, obtuse at apex, slightly curved

upwards, sparsely haired. Abdomen of ♀ lanceolate. Anatomy of adult: Ovaria drop-shaped, terminal filament absent. Ecology: Occurrence in forest habitats, intermediary and steppe habitats. Host range: Various aphid groups except the Lachnidae. Distribution: Widely or less distributed species. Fossil relatives: † *Pseudaphidius* STARÝ, † *Protodiaeretiella* STARÝ(?). The connections seem to be clear as for the wing venation in the first mentioned genus, nevertheless, the smooth propodeum in species of † *Pseudaphidius* and areolated or carinated propodeum in *Aphidius* represents a difficulty in solving this relationship. Present relatives: A separated group, probably progressive as to the phylogeny.

Group 9: *Diaeretiella* STARÝ

Embryology: Unknown. Bionomics: Pupation inside mummified aphid. Morphology of adult: Wing venation of *Diaeretiella*(?) type (♂♂ of some species) or more reduced. Antennae with low number of segments which is different in both sexes. Notaulices deeply developed anteriorly. Propodeum areolated. Ovipositor sheaths comparatively short, obtuse at apex, somewhat curved upwards. Abdomen of ♀ lanceolate. Anatomy of adult: Unknown. Ecology: Occurrence in forest undergrowth, peatbogs and wet places. Host range: Some aphid groups (except the Lachnidae). Distribution: Europe. Fossil relatives: Unknown. Present relatives: It might have some relation to *Aphidius*.

Group 10: *Lysiphlebus* FÖRSTER, *Lysiphlebia* STARÝ & SCHLINGER

Embryology: Eggs lemon-shaped. Distinct adaptation to parasitism similarly as in *Aphidius*. Instar I larva with simple cauda. Bionomics: Pupation inside mummified aphids. Emergence hole in the dorsal portion of the mummified aphid. Morphology of adult: Wing venation of *Lysiphlebus* (subg. *Phlebus*) type and more reduced. Antennae with low number of segments, which is different in both sexes. Notaulices developed anteriorly. Propodeum areolated, carinated or smooth. Ovipositor sheaths comparatively short, narrowing to the apex, slightly curved upwards, sparsely haired. Abdomen of ♀ lanceolate. Anatomy of adult: Unknown. Ecology: Occurrence in forest type, intermediary and steppe habitats. Host range: Various aphid groups with exception of the Lachnidae. Distribution: Mostly widely distributed species but some genera are apparently vicariant (*Lysiphlebus* x *Lysiphlebia*) in distribution. Fossil relatives: Unknown. Present relatives: it is an isolated group. Certain but only morphological similarity with a part of *Aphidius* group.

Group 11: *Paralipsis* FÖRSTER

Embryology: Unknown. Bionomics: Pupation inside mummified aphid. Emergence hole in the dorsal part of the mummified aphid. Morphology of adult: Wing venation of *Paralipsis* type. Antennae with higher number of segments, which is different in both sexes. Notaulices distinct anteriorly. Propodeum smooth. Ovipositor sheaths comparatively long, wide, obtuse at apex, almost straight. Abdomen of ♀ widely oval. Anatomy of adult: Unknown. Ecology: Occurrence in steppe type and intermediary habitats. Host range: Parasites of various groups of root aphids. Close connections with ants (mutualism). Distribution: Not too widely distributed species. Europe, Far East. Fossil relatives: Unknown. Present relatives: Unknown. A quite isolated and specialized group.

Group 12: *Aclitus* FÖRSTER

Embryology: Unknown. Bionomics: Pupation inside mummified aphid. Position of the emergence hole unknown. Morphology of adult: Wing venation of *Aclitus* type. Antennae with low number of segments, which is different in both sexes. Notaulices distinct anteriorly. Propodeum smooth. Ovipositor sheaths narrow, straight and comparatively long. Abdomen of ♀ rounded. Anatomy of adult: Unknown. Ecology: Occurrence probably in forest and intermediary habitats. Host

range: Probably parasites of various groups of aphids. Distribution: Europe, Far East
Fossil relatives: Unknown. A very isolated group.

Group 13: *Monoctonus* HALIDAY, *Monoctonia* STARÝ

Embryology: Instar I larvae with simple medium size caudal appendage. Bionomics: Pupation inside parasitized aphid. Emergence hole in the dorsal portion of the mummified aphid. Morphology of adult: Wing venation of *Monoctonus* type and more reduced. Antennae with low or higher number of segments, which is different in both sexes. Notaulices developed anteriorly. Propodeum areolated or carinated. Ovipositor sheaths downwards curved, of various shape, sparsely haired. Abdomen of ♀ lanceolate to rounded. Anatomy of adult: Unknown. Ecology: Occurrence in forest and intermediary types of habitats, mostly of humid character. Host range: Various aphid groups except the Lachnidae. Dependence on the mode of host life various. Distribution: Wide distribution is rare. Fossil relatives: † *Promonoctonia* STARÝ(?). Present relatives: It seems to be an isolated group.

Group 14: *Trioxys* HALIDAY, *Acanthocaudus* SMITH, *Bioxys* STARÝ & SCHLINGER.

Embryology: Eggs lemon-shaped. Instar I larva with short simple caudal prong. Bionomics: Pupation inside mummified aphid. Emergence hole in the apical portion of mummified aphid. Morphology of adult: Wing venation of *Trioxys* type. Antennae with low number of segments, which is different in both sexes. Notaulices distinct anteriorly. Propodeum areolated, carinated or smooth. Ovipositor sheaths downwards curved, of various shape; accessory prongs or prong on the last abdominal tergite developed. Abdomen of ♀ lanceolate to subrounded. Anatomy of adult: Ovaries widely oval. Ecology: Occurrence in forest, intermediary and steppe type habitats. Host range: Mostly more or less strictly specialized species. Parasites of various aphid groups except the Lachnidae. Distribution: Mostly restricted. Fossil relatives: † *Protacanthoides* MACKAUER, † *Palaeoxys* MACKAUER. Present relatives: An isolated and specialized group. Some subgroups may be recognized inside the genus *Trioxys* HALIDAY but only of subgeneric value.

Group 15: *Lipolexis* FÖRSTER.

Embryology: Instar I larva with rather long and curved caudal prong and two oblique short accessory prongs. Bionomics: Pupation inside parasitized aphid. Emergence hole in the dorsal part of mummified aphid. Morphology of adult: Wing venation of *Lipolexis* type. Antennae with low or higher number of segments, which is different in both sexes. Notaulices distinct anteriorly. Propodeum areolated or carinated. Ovipositor sheaths curved downwards, narrowed to the apex. Abdomen of ♀ lanceolate. Anatomy of adult: Unknown. Ecology: occurrence namely in steppe and intermediary habitats. Host range: Parasites of a number of aphid groups except the Lachnidae, to a lesser degree strictly specialized parasites. Distribution: Widely or less distributed species. Fossil relatives: Unknown. Present relatives: Very isolated group. The similarity in wing venation with that of *Trioxys* is only of convergent value.

BIOLOGICAL CONTROL. The general conclusions of our studies seem to clearly indicate the relative importance of the research of the phylogeny of the group for biological control. The research of phylogeny of the group helps us to establish the main trends of development of the group, which enables the general evaluation with respect to biological control. Were the parasites a group with the main trend to parasitize coniferous aphids, there would be hardly any chance to apply them as biological control agents in control of aphids in deciduous orchards, field crops, etc. The classification of the group as a progressive group, its progress being connected with the progress of their hosts, the aphids, is rather valuable just owing to the mentioned

the trend of aphid development to steppe zone, which is mostly cultivated important as it shows the increasing importance of aphids as pests. This has generally been shown by many aphidologists (KENNEDY & STROYAN, 1959, KOV, *et al.*, etc.). Better said, the aphids have become—although there are very few species—also widely distributed pests in the tropics, in a zone, which had originally only poorly inhabited; nevertheless, the cultivation of the growing of monocultures of crops on extensive areas (cotton, etc.), suitable conditions, etc., created apparently a rather suitable environment for the presence of some pest species. The knowledge of phylogenetic relations of the aphids might help in selecting, introducing and establishing parasite species in a control program.

5. 69, 75, 143, 183, 221, 233, 286, 323, 337, 521, 527, 586, 618, 693, 696, 712, 728, 737, 740, 758, 796, 866, 937, 975, 978, 981, 983, 1008, 1020, 1003, 1015, 1130, 1137, 1182, 1191, 1255, 1261.

CHAPTER VIII

Distribution

bution is usually mentioned as a population attribute which involves the frequency of a number of places by a number of individuals at a given time or over an period of time (CHIANG 1966). Distribution in the latest sense is usually divided into the three following categories: (1) Geographic distribution, (2) Habitat distribution, (3) Microhabitat distribution.

In our opinion it is not possible to separate the three categories from each other, as they are mutually dependent and influenced. For this reason, distribution is dealt with in the broader sense in this chapter.

The first attempt to classify the geographic distribution of the Braconidae (not including the Aphidiidae) was made by TELENGA (1952). He undertook the research on phylogeny, morphology and geographic distribution to distinguish a number of taxonomic complexes occurring in the Palearctic fauna. Nevertheless, in accordance with the pioneer character of this direction of work various conclusions may be generalized. When characterizing the separate faunistic complexes of parasites, either geographic distribution or geological history has been applied to a different degree, which has led to a certain inadequacy in the classification. This is no doubt caused by the lack of more detailed records on the biology of separate species except for general data, on the other hand, the hosts of the Braconidae belong to various insect orders. The present fact requires both the classification of the effect of factors that influenced the distribution of these groups, and the geographic distribution of the parasite, and the relationship. This would complicate the whole matter even if sufficient data were at hand. Better to say, similarly as in other groups of parasitic insects, both the host and parasite phylogeny relationship and the ecology of the host irrespective of taxonomic affinities, have a deep influence on the specificity of separate groups of parasites (wood-borer parasites, etc.).

TELENGA's main conclusion, the general rule that parasite fauna is connected with certain communities and zones (steppe, forest), has been followed by several workers. When we use the re-classified TELENGA's principles in the aphidiid parasite group, we find a great advantage because of having used mostly reared material (exact knowledge of host, host plant, habitat, etc.). Further, the aphid parasites attack the aphids exclusively and thus the influence of too wide a host range is eliminated (parasitization of members of various insect orders, etc.); the main directions of aphid phylogeny seem to be known; the phytogeography has been found to be extremely helpful; the parasite group is not too numerous, so that we have been able to cover the known world fauna of parasites on a corresponding level of present day knowledge.

One viewpoint has to be stressed in addition. The aphid parasites have to be

classified in an objective way, as far as possible. Our obviously best knowledge of European fauna, when being compared with the other parts of the world, could cause the usual mistake of classifying Europe as the centre of origin and distribution of the group, most of the genera and species being known from there. We have tried to show how untrue such a classification would be from many viewpoints.

Originally, a faunistic complex was classified by TELENGA (1952) as follows: 'Faunistic complex is a certain group of species that is characterized by more or less identical conditions of existence and geographic distribution.'

In our opinion, this definition does not suit the true classification of a faunistic complex because of the misdefining of this term. The following two terms must be distinguished:

Fauna (BOBRINSKIY, 1951): 'Fauna is a complex of animal forms, which has developed and has been consolidated by an identical area of distribution'.

The fauna of a given area is composed of separate faunistic complexes. A faunistic complex has to be classified as a complex of animal forms that are consolidated by identical origin and recent area of distribution.

Only typical species have been used in the classification of separate faunistic complexes of the Aphidiidae of the world.

History of Floras and Faunas

As we have ascertained that there is a deep developmental connection of the parasites with the floristic zones, it is necessary to present some short notes on the general history of world floras to understand the classification of faunistic complexes of parasites.

- HISTORY OF WORLD FLORAS. (Generally after ALJOCHIN et al., 1961). Since the Mesozoicum, the main centers of origin of tropical forest flora have been distinguishable: Neotropical, palaeotropical, African and Malaysian. The two first groups were connected at the place of the present day Atlantic ocean. The connection of Africa with Hindustan was due to the hypothetic land, Lemuria, running along Madagascar. These connections partly represented the inheritance of the ancient Gondwana, partly they developed later again.

Similarly, of the Pre-tertiary age, were the connections among the floras of Antarctica on the one hand and floras of Australia, South Africa and Antarctic America on the other.

In the northern hemisphere, the flora of Europe and Asia had been separated from the tropics from ancient times by the wide Mediterranean sea Tethys. In the eastern borders of Asia the districts of Tertiary tropical forests were connected directly with the tropical flora of Malaysia. The subtropical flora spread from the Chinese-Japanese subregion westward to the true Mediterranean following the Himalayan route. We may presume that the tropical forest flora—Poltavian flora—was distributed along the shore of the Tethys sea over large areas from Asia to southern Europe. The deciduous forests spread from eastern Asia following the Saian route of migration. There are the Turgayan forests, which transitioned into the coniferous forests at the North that were distributed to the shores of the Arctic ocean at the Upper Tertiary.

The mountain taiga had been distributed in the mountains in the arcto-tertiary plain forest zone since the beginning of the Tertiary. In the Far East, the coniferous forests had been developing in the Beringia land area and from here they spread westwards to Asia and eastwards to North America.

Considerably later, at the end of the Tertiary, various types of desert and desert-steppe flora had spread along the shore of the dessicating Tethys sea. The main desert centers were: Gobi, Central Asia, Iran, North Africa, Arabia and the desert Tar. The flora spread from these centers over the whole of the ancient Mediterranean.

The original centers of ancient pre-glacial steppes were the centers where the present day Mongolia and North America are situated.

The history of floras in the Quaternary is rather complicated, being presented here only very briefly: In the territories that were not entirely glaciated (e.g. Transbaikalia) cool steppes occurred in the Pleistocene. The forest flora was preserved in the west of Eurasia in the refugia (Transcarpathian, South-Ural, Altai-Saian) in the period of Quaternary glaciation. After the retreat of the pleistocene glaciers, there was the tundra at that place, sometimes with districts of periglacial open woodland. The forest formations that had spread from refugia gradually formed the present forest zone with its numerous subdivisions. The glacial refugia were represented by the territories of Atlantic Coastal America and the Pacific coast northward to Mexico in N. America. The steppes of North America (prairies) had originated in the Cretaceous and at the beginning of the Tertiary. On the contrary, European steppes formed as a zone in the post-tertiary period. The western tundras are comparatively young. If there occurred tundra flora in the North of Yakutia and in Arctic America at the end of the Tertiary, then in the districts of the present day tundra zone territories, the forests were predominant in the other parts of Eurasia. The formation of circumpolar tundra zone similarly as that of the coniferous forest zone at their recent limits is of post-glacial periods.

Because of the origin of aphids and their contemporary distribution with respect to the classification of faunistic complexes of the aphidiid parasites, it is necessary to deal with the history of Holarctics and the Far East in more detail.

— *Holarctic flora.* In the ancient periods of the geological history in Palaeozoic and Lower Mesozoic, the floras were relatively homogeneous all over the land surface. In the Cretaceous, the break-up of the flora had begun: In North-eastern Siberia, it forms the centre of origin of the Coniferous, which spread in the Tertiary to Northern Asia and N. America. The development of floras of Angiosperms began at the end of the Cretaceous, probably in various parts of the world. The antiquity of the Tertiary ocean Tethys, which separated northern land from tropical continents, did not enable the direct connection of tropical floras with non-tropical floras, except for districts of south-eastern Asia.

In the Miocene period the arcto-tertiary flora was distributed over large areas from Greenland to the shore of the Mediterranean sea (*Quercus*, *Fagus*, *Juglans*, *Populus*, *Ficus*, *Ginkgo*). Just from this Neogenous flora the subtropic, deciduous and coniferous forest flora of the Holarctics had differentiated.

In the Miocene, the Paltavian flora was distributed in Europe, being rather rich, similar to tropical flora of southern Asia (*Ficus*, *Myrtaceae*, *Lauraceae*, etc.). Northward this flora, Turgaian flora was distributed over Europe and almost all non-tropical Asia. It resembled the recent relic forests of eastern China, Transcaucasia and Atlantic coastal N. America (deciduous, evergreen, coniferous: *Quercus*, *Acer*, *Fagus*, *Populus*, *Magnolia*, *Nerium*, *Punica*, *Laurus*, *Ginkgo*, *Sequoias*, etc.).

At the end of the Tertiary, boreal coniferous forests had separated (from the European species of *Larix*, *Picea*, *Abies*, *Salix*, *Corylus*, *Betula*, *Alnus*). These forests had spread southwards from the Arctic ocean owing to the cooling of the climate.

Thus, during the Tertiary, three zonal types had originated from one homogeneous arcto-tertiary flora: Paltavian, Turgaian, Boreal.

Neither tundra, nor steppe were present in the typical zonal distribution in pre-

glacial Europe except the steppe district near the Caspian. The true plain steppes occurred only in the Transbaikalia, N. Mongolia, and in Gobi.

The general cooling, covering all the non-tropical territory from the end of the Tertiary, and then the following Quaternary cooling because of glaciation in the North, principally changed the distribution and deeply influenced the composition of the Holarctic floras.

The Paltavian flora had gone because of lack of southward migration possibilities due to the existence of the Mediterranean sea. But on the eastern borders of the continents of N. America and Asia this flora had the possibility partly to survive as there was not the destroying influence of progressing glaciation. The present Chinese-Japanese, N. American Atlantic Coastal, and Macronesian forest floras had originated to a great extent from this flora.

The Turgaian flora, because of the progressing pressure of the boreal coniferous forest, had also retreated. The main refugia of this flora and from which deciduous and mixed forests originated, were the Far Eastern and Pacific Coastal districts, similarly as the sloped Appalachian mountains in N. America and the Transcarpathian and S. Ural districts. The invasion of boreal coniferous forests from the north and invasion of dry semideserts and dry steppes from the south entirely destroyed the forest of turgaian type in all the great areas from Ural to Amur. Only some localities of relict forests (Tilia), still occurring in the eastern submountains of Ural and in Alatau, represent the rest of the past continuous belt of deciduous Tertiary forest in southern Siberia.

The separation of old pre-glacial floras was also caused by the origin and distribution of Alpine foldings in Eurasia and N. America.

The progressive drying of the climate occurred in the Quaternary. The dessicating territories occurred in inter-glacials for example and were distributed from C. Asia to Asia Minor and in the south west to N. Africa; the Ancient Mediterranean had originated, with the flora of desert, dry steppe, dry forest types.

- *Far Eastern flora.* Similar to the tropical equator flora, the Chinese flora, at least from the Tertiary, has developed at the very place of its present distribution area. From there, as from the centre that connected refugia both of forest subtropics and boreal floras, deciduous and mixed forests of Eurasia, similar to the Larix- and other forests of Siberia had spread westwards and northwards in the Tertiary.

The spread of deciduous and mixed forests (Fagus, Quercus, Tilia, coniferous) westwards follows the mountains of southern Siberia over the Saians and Altai mountains and further over S. Ural to Europe (*Altai-Saian migration route*).

The second, southern migration route of east Asian forest flora followed the slopes of the mountains of C. Asia and the Himalaya to Tian-Shan and further to the Caucasus and the territory of the European Mediterranean (*Himalayan route*).

Both these routes enriched the subtropical and deciduous forests of arcto-tertiary origin, which were distributed at that time in pleistocene Europe.

Then, continuous zones of coniferous, deciduous and subtropic forests of Eurasia moved to the south and the two latter types were separated by the glaciation, and by dessication of C. Asia.

If we summarize the history of floras and plant kingdom at all, it is obvious that the plants had almost "covered the environment" at the Tertiary. The Quaternary caused a strong reduction. The present day period may be characterized as a period of convalescence due to the effects of the Quaternary. For this reason the plants are a progressive group of today, which is in connection with the "development" of new taxa.

Every host group development is followed by the development of parasitic forms.

When we have mentioned the progressivity of plant kingdom, the same must be true for the parasites of plants—the aphids, and all the aphids—natural enemies food chain.

—*Principles of plant geography.* The main principles of plant geography are mentioned below, being important for the classification of parasite faunistic complexes (GOOD, MASON, after CAIN, 1944):

A. Principles concerning the environment.

1. Climatic control is primary.
2. Climate has varied in the past.
3. The relations of land and sea have varied in the past.
4. Edaphic control is secondary.
5. Biotic factors are also of importance.
6. The environment is holocenotic.

B. Principles concerning plant responses.

7. Ranges of plants are limited by tolerance.
8. Tolerances have genetic bases.
9. Different ontogenetic phases have different tolerances.

C. Principles concerning the migration of floras and climaxes.

10. Great migrations have taken place.
11. Migrations result from transport and establishment.

D. Principles concerning the perpetuation and evolution of floras and climaxes.

12. Perpetuation depends upon migration and evolution.
13. Evolution of floras depends upon migration, evolution and environmental selection.

—*Climate.* A brief review of the main types of climate of the earth is mentioned below (after SCHMITHÜSEN, 1961), being important for the classification of floristic zones—parasite distribution as well as for parasite introduction principles.

1. Climate of perpetually moist tropics.
2. Periodically dry climate of moist subtropics.
 - (a) with short dry period
 - (b) with long dry period
3. Periodically moist climate of dry tropics
 - (a) with long rainy period
 - (b) with short rainy period
4. Absolutely dry tropical or subtropical climate.
5. Periodically moist climate of dry subtropics
 - (a) with very short rainy period
 - (b) with longer rainy period
6. Climate of moist subtropics
 - (a) climate of winter rains and dry summer
 - (b) subtropical climate with moist summer
 - (c) perpetually moist subtropical climate
7. Absolutely dry climate of temperate zone
8. Periodically moist climate of temperate zone
 - (a) climate of semi-desert
 - (b) climate of steppes
9. Climate of temperate zone with uniform precipitations during the year
 - (a) extremely oceanic
 - (b) from mild oceanic to mild continental
 - (c) from continental to extremely continental
10. Subpolar climate
 - (a) subpolar oceanic climate
 - (b) subpolar continental climate
11. Polar climate

— *Floristic formations.* As the general knowledge of the world fauna of parasites is far from being complete, the separate faunistic complexes being connected with separate floristic zones, a brief review of floristic formations (after SCHMITHÜSEN, 1961) is presented to allow a better orientation of the reader.

I. Forests.

Evergreen rain forest.

Tropical evergreen rain forest of lowlands (In lowland districts of continuously moist warm tropics).

Tropical evergreen mountain cloud forests (In continuously moist tropics and cloud districts of tropical mountains ~ mostly 1000-3500 m).

Subtropical evergreen rain forest (Gradual transition to tropical forest being very similar to the latter).

Temperate evergreen rain forest (partly similar to the subtropical rain forest).

Evergreen sclerophyllous and coniferous forests.

Sclerophyllous forests (evergreen sclerophyllous forest, type of subtropical districts with winter rainy period).

Laurel forests (Mainly in cloud districts of subtropical submountains, inter-zone between sclerophyllous forest and rain forest of temperate zone).

Boreal coniferous forest (Mostly or entirely from conifers).

Mountain coniferous forests (In various climatic zones).

Mangrove forest (In saline grounds of tropical sea shores).

Deciduous forests.

Deciduous mesophytic summer forests (In districts with cold winter and long moist and warm vegetation period, often mixed with conifers).

Tropical deciduous rain forest (In monsoon Asian districts for example).

Tropical xerophytic deciduous forest (Inter-zone between monsoon forest and dry forests).

Xeromorphic forests.

Thorn forests and succulent forests (With a number of succulent and thorny plants, in tropics and subtropics, where there are 8-9 months with no rain, only low precipitations during a rainy season).

II. Scrub formations.

Evergreen scrub formations.

Hydro- and mesomorphic evergreen scrub formations (temporary, in development of secondary forest in continuously moist tropics).

Coniferous elfin woodland (On upper forest limit, as well as associations on moors).

Sclerophyllous scrub formations (namely in subtropics with rainy winter periods).

Xeromorphic scrub formations.

Thorn and succulent scrubs (As mixed, often evergreen, often deciduous).

Deciduous scrub formations.

Formations of deciduous summer scrubs of temperate and subpolar belts (subarctic elfin woodland, and subantarctic scrub formations).

III. Savannas and steppes.

Savannas (tropical grassy areas).

Flooded savannas (covered with water, mostly natural, usually with no trees, along tropical rivers, inundation zone).

Moist savannas (periodically green tropical areas, covered by tall herbaceous vegetation).

Termite savannas (park woodland - with peculiar floristic formations around the termite nests).

Dry savannas (grassy areas, in lowlands of tropical zone).

Thorny savannas (in very dry districts).

Steppes of temperate zone.

Prairies or chernozem steppes (widely distributed in temperate moist areas with dry summer and cold winter periods. Mostly cultivated today).

Dry steppes of temperate zone (short grass and halfscrub steppes, transitional zones from prairie to semi-desert).

IV. Meadows.

Meadows and allied formations (in more or less moist oceanic climate of temperate zone with no hard winters and without strictly defined dry periods. Mostly cultivated, developed under man's activity and preserved in the present state due to continuous activity of man—cutting, pasturing etc. To natural meadows, some saline and swamp meadows, and mostly bottomland meadows).

Alpine and subpolar meadows

Saline meadows (sea shore)

Bottomland meadows

Moist meadows

Fertile meadows and pasture meadows, etc.

Reed thickets and herb meadows

Reed thickets on ponds

Reed thickets near springs

Tall herb meadows

Meadows near springs

V. Formations of undershrubs and semi-undershrubs.

Semideserts (Semi-arid and arid areas, xeromorphic open plant associations: Low bush semidesert, succulent semidesert, semidesert with halophytes, etc.).

Saxicolous formations and formations of solid grounds (Plant formations of rocks, alpine formations of rocky screes, rocky tundras or arctic meadows, etc.).

High moors

Peat moss bogs

Tundra mires

VI. Formations of mesophytes.

Ephemeric herb meadows (Annual grasses in deserts after rains, etc.). *Herb meadows on muddy soils.* *Formations of field weeds* (Autochthonous formations of field weeds).

VII. Deserts.

The true deserts are districts of land with no or with scattered plant cover. There is no strict limit between desert and semidesert).

VIII. Formations of water reservoirs.

IX. Formations of seas.

— HISTORY OF WORLD FAUNAS. Only some principles have been mentioned that need to be stressed to understand the classification of the faunistic complexes of parasites. (Formation of the main continental faunas, after BOBRISKIJ, 1951; some of these seem to be true for the Vertebrates only, author's note).

1. In the North-southerly direction the faunas of different parts of land, occurring at the same latitude, gradually acquire greater differences.

The fauna of the tundra of Europe, Asia and America is unusually identical in all the zone, the main part of animals being circumpolar in distribution.

Faunas of taiga (coniferous forest, etc.) of Eurasia and N. America are still rather related, having many identical elements, some great differences occurring, too.

The faunas of the Mediterranean, C. and Inner Asia, and the Far East differ among themselves, and from the faunas of the southern parts of North America. The differences are, however, of a subregional level.

2. The most ancient animals of the period of the present day occur in the areas south of the tropic of Cancer.

3. Many groups, restricted today in their distribution to regions situated south of the tropics, may be known as fossils from the north of the tropics. On the contrary, animals occurring today north of the tropics of Cancer, are not known as fossils south of the tropics.

4. Animals usually transferred from the northern to the southern hemisphere in corresponding environmental conditions, usually become established, but generally not vice versa.

5. The main direction of the exchange of faunas is North-South, but not vice versa.

In case of the disappearance of barriers (climatic, geological, etc.) one fauna comes into contact with another one. Complicated processes originate in consequence, having different results.

(a) The elements of both faunas are exchanged in about the same degree, new fauna originating.

(b) One fauna, which is more adapted to the given conditions or is better organized, suppresses the other.

In this case, separate forms of the retreating fauna may remain as relics.

The changes and migrations of faunas develop at various speeds. After the disappearance of the barrier each fauna may conserve its independence for a certain time. And on the contrary, one fauna, the distribution of which is separated into two by a physical barrier, may conserve its independence for a long time.

Aphid Phylogeny

When classifying today's distribution of aphids all over the world it is obvious they are mainly distributed in the temperate climate belt of the northern hemisphere, only some groups being typical for the tropics. Their recent distribution is easily understandable as the aphids have been connected with the mentioned type of climate also during their evolution.

The climate and flora play the main role in the distribution of aphids. SHAPOSHNIKOV (1951, etc.) reached the following conclusions on bases of classification of aphid evolution and evolution of their host plants: the main direction in aphid evolution is connected with their transition from coniferous to deciduous trees, from trees to shrubs, from trees and shrubs to herbs, with no dependence on phylogenetic relationship and age. This corresponds to the general direction of plant evolution. The main cause of a similar direction of evolution is the same both in the plants and aphids—the adaptation to the occurrence in conditions of a drier climate.

The most ancient groups of aphids are really connected with trees, just with those that are typical of a forest zone—with coniferous, Fagaceae, Salicaceae, Ulmaceae.

In the forest zone, in contradiction to the fauna of steppes and deserts, the ancient aphid groups are more distributed and the younger groups less. For example, in the forest zone, aphids of the ancient groups occur—the Adelgidae, Mindaridae, Lachnidae, which live mostly on conifers, the chaetophorids (Atheroidinae) on *Betula* spp., etc. The species of the mentioned groups are, however, absent in the steppe and desert zones, although their host plants sometimes occur here. On the other hand, in the forest zone the numerous species of the evolutionarily youngest aphid groups that are connected with herbs are lacking—*Macrosiphoniella*, *Turanosiphon*, *Cryptosiphum*, etc., similarly to numerous species connected with Gramineae (*Siphia*, etc.).

further, xerophyllous forms of *Xerophilaphis*, *Smiela*, *Xerobion*-type, and also the genera that are connected with halophilous plants.

The geological history of the earth had the basic influence on plant communities of separate continents. Temporary connections, land bridges, climatic changes, etc., have all impressed deep features on the contemporary flora of the world. Aphids have naturally been influenced in a similar way, although their spread has also been influenced by several other factors (air streams, etc.). Because of the main distribution of aphids in the temperate areas of the northern hemisphere, the glaciation in the Quaternary has apparently deeply influenced the aphid fauna. Most of the territory of Europe was covered by glaciers. The original native fauna of these districts either died or migrated to the southern parts of Europe because of the gradual movements of the glaciers to the south. As was mentioned in a previous chapter, the glaciation had primarily influenced the flora, various communities being influenced in a different way, another zonation having developed, and all this had an influence on aphid fauna. Nevertheless, in the post-glacial periods, because of the retreat of the glaciers to the north, and also in the interglacial periods, the flora had spread again to the new territories and followed, in accordance with a certain zonation, the glaciers.

The migration of host plants has caused some changes in the aphid fauna. Some of the species, because of the lack of hosts, occur in the southern parts only. Other species spread northward, but their primary host plants did not; such species occur today as anholocyclic species in Europe, being, however, holocyclic in the south, where both primary and secondary host plants occur. In other cases, the distribution areas of host plants and aphids are identical.

Parasite Phylogeny

As mentioned previously, the aphidiid parasites have originated from the Ichneumonoid complex of the Hymenoptera, being connected with the braconoid group that apparently originated in the tropics. Some groups of this braconoid complex, which is mostly classified as the family Braconidae today, had, however, differentiated and developed clearly in the temperate climate zone, where also their center of development might be ascertained. One of these groups mentioned is the parasite family Aphidiidae.

The group of aphidiid parasites has developed in close connection with the host group—the aphids. Nevertheless, the fact has to be stressed that both the groups have on the one hand their own phylogenetical directions, on the other hand, there was of course a deep influence of the host groups on the parasitic groups as a part of the environment of the parasites (see: Host specificity).

If the present relations of the groups of aphids and parasites are classified, there is no doubt that no parasite species of the family Aphididae attack members of the aphid superfamily Adelgoidea (families Adelgidae, Phylloxeridae). This means, as to the phylogeny, that the parasite group adapted to the parasitism on aphids at the period when the main two groups of aphids—the Adelgoid and the Aphidoid—had differentiated. This is also recognizable from the comparison of morphological and ecological features of both groups.

We do not know the ancestors of the recent aphidiid parasites that represent the original groups and adapted to the parasitism on aphids. Judging from the present distribution and specificity of the parasite group, it is, however, obvious they originated in a temperate climate belt and in forest type habitats.

Although it is difficult to recognize the development of separate genera of the

aphidids as the species of these genera often attack a number of various phylogenetically unrelated groups, the aphid ecology being also very important, the basic fact has to be stressed that there is no doubt about the existence of two main phylogenetic directions in the parasite group (further details—see Phylogeny).

A. The first group is represented by the ancestors of the present genera *Pauesia*, *Xenostigmus*, *Diaeretus*, *Metaphidius*. They are parasites of the Lachnidae, being connected primarily and mostly with coniferous forest habitats.

B. The second group is represented by ancestors of the rest of the parasites. They are primarily connected with the deciduous forest habitats and the aphids occurring there.

The first group, the ancient coniferous forest complex, had developed very separately and has given origin to a few complexes that are, however, closely connected again with the coniferous forest type.

The second group, the ancient deciduous forest complex, on the contrary, has given origin to the steppe fauna. The adaptation of a certain part of this complex to the conditions of a drier climate have no doubt caused big changes and evolution of new forms. The recent deciduous forest and the steppe complexes are the most numerous as to distribution, spread, number of species, etc. For this reason, the phylogenetic direction deciduous forest — steppe seems to be the main and typical direction of the aphid parasites development.

From the steppe complex, the semi-desert and desert complexes have originated. The fauna of the ancient steppe areas is but poorly known to give any more detailed opinions.

Some elements of the deciduous forests seem to have adapted to the conditions of a cooler climate. These are today's faunistic complexes of Forest Tundra and Boreal Europe, which are probably the results of adaptation to the conditions of cool arctic steppe (tundra) or to the transitional type (forest, tundra).

On the other hand, some elements of the ancient deciduous forest that was connected with the tropical rain forest (south-eastern Asia) invaded the latter type of forest and apparently adapted themselves as the parasites of certain aphidoid groups of aphids that occurred there. It is possible, the adaptation was either of the common type, aphidoid type, or on the derived and more specialized groups (Greenideidae) as it seems from the composition and host specificity of the recent parasites of the mentioned groups.

— DISTRIBUTION OF THE PARASITES. The general distribution of the aphid parasites is determined by the following main factors: (1) The geological history of earth, (2) The phylogeny and distribution of floras, (3) The phylogeny of the parasite group itself (or higher taxonomical unit—braconoid group, etc.) (4) The phylogeny and distribution of aphids, (5) Man's agency.

The separate factors are dealt with in more detail in different chapters of the book. — *Aphids and parasites*. The following possibilities of host — parasite distribution relationship may occur:

A. Host is not attacked by the parasites at all.

This may be either the result of our poor knowledge of the parasites, or there may be really a group of aphids disregarded by parasites (*Adelgidae*, *Phylloxeridae*).

B. Host is attacked by aphid parasites

(a) An aphid species is attacked by the same parasite species in its whole distribution area. Examples: *Brevicoryne brassicae*—*Diaeretiella rapae*. *Schizolachnus pini*—*Pauesia unilachni*.

(b) An aphid species is attacked by the same parasite species in a part of its distribution area only. This may be caused either by the spread of the aphid (man's

agency) over a geographic barrier (ocean), or it may be caused by different requirements on the environment by the host and parasite. Example: *Therioaphis trifolii* and its parasites.

(c) The aphid species is attacked by the same parasite species in all its distribution area and by other parasites in some parts of it. Examples: *Brevicoryne brassicae*—*Diactroetiella rapae*—other parasite species in different districts of the host aphid distribution area.

(d) The parasite fauna of an aphid species is different in various parts of its distribution area. Examples: *Hyalopterus pruni*, *Toxoptera aurantii*, *Aphis craccivora*, *A. gossypii*, and numerous other cases.

— *Center of origin.* Paleontology is usually found to be most helpful in identifying the center of origin and center of distribution of a given group. These methods can, however, be applied very poorly in the aphidids because of lack of material.

In such a case, the centres are identified on the bases of the following theses, commonly used in zoogeography:

1. The districts where the most primitive forms of the given group occur, i.e. forms that are little different from the original forms, is the center of origin, and also the center of distribution in this case.

Good taxonomic knowledge is necessary for such a classification. Nevertheless, and this is a disadvantage of this method, all the recent forms are more or less deviated from the original (fossil) direction, as may be recognized from the comparison of fossil and recent fauna. Besides, evolutionarily younger forms may be found to occur today in the present area of such a centre of origin.

2. The district, where the highest number of forms of the given group occurs, is usually the center of distribution.

This is in close connection with a good state of knowledge which is not the case of the aphidids and incorrect results would be obtained when comparing the clearly unequally studied faunas of different regions.

3. The center of origin might be a district that corresponds by its environmental conditions to the life of the original group.

This is useful in the case of aphidids.

Summarizing the generally used criteria, because of our contemporary state of knowledge, we shall deal with that stage of phylogeny of the aphidids, when the ancient deciduous forest and coniferous forest complexes were separated. More detailed information was given in the chapter about parasite phylogeny and host specificity development.

Although we know some fossils from the Upper Tertiary, we prefer to start classifying the centers of origin from the recent distribution of the aphidids.

Deciduous forest. The ancient faunistic complex occurring in the Turgai forest seems to be the basic one as to the origin of the present fauna. We do not know the corresponding fossils, but due to the possibility of comparison of known Far Eastern and European fauna, conclusions may be reached that the generic range of this fauna was very similar to that of the present fauna. The more ancient faunas (Oligocene) possess a lot of characters that enabled us to separate them as ancestors of the present forms (comparison of these faunas see Phylogeny). In the Turgai forest there occurred at least species of the genera *Ephedrus*, *Toxares*, *Praon*, *Protaphidius* (secondary, an element of coniferous forest), *Aphidius*, *Lysiphlebus*, *Lysiphlebia*, *Trioxys*, *Monoctonus*, etc. The influence of the Quaternary caused the migration and disjunction of the turgai forest belt. It has remained in a more or less untouched state up to the present day in the Far East. The central part was suppressed, in Europe it has given origin to the recent European Deciduous Forest fauna. The disjunction

of the primary homogeneous belt has given origin to the two complexes of today, which are connected with the deciduous forest formation: the first one is older, having existed since the end of the Tertiary to the present day, the second one is secondary, younger. From these two main centers of origin a further spread of the species in the neighbouring zones and habitats may be derived. The third center, the third rest of the tertiary deciduous forest, seems to exist in N. America.

A further spread from these centers that followed, invaded (a) the tropical rain forest (this invasion may be, however, of Tertiary age), (b) the steppes (the invasion, because of the origin of steppes in Eurasia, seems to be of Late Tertiary, interglacials and post-glacial periods). The center of origin of the steppe fauna was somewhere in western Eurasia. From this centre of origin the species spread to the semidesert and desert, partially to intermediate zones (forest-steppe). In quite recent periods they invaded the cultivated lands, which have originated as a result of forest cultivation (western Europe, etc.). The Neartie steppe fauna is ecologically identical, nevertheless, there occur certain specialized elements that are not present in Eurasia (*Acanthocaudus*). As for the generic composition, it seems that it originated from a source similar to the Eurasian steppe faunas. (c) forest tundra; this invasion is clearly of interglacial and postglacial period.

Coniferous forest. Two centers of conifers are known today. The first one being somewhere in C. China, the second one in Neartie America. Because of the existence of the identical main generic complex both in Eurasia and Neartie America, it is clear that the separation of coniferous forests had begun at the period when there occurred ancestors of the recent Cinarine aphids and their "*Pauesia*-like" parasites (see history of floras). *Pauesia* and *Diaretus* are no doubt the original groups of the coniferous forest parasite fauna.

In N. America, there is a derived genus, *Xenostigmus*, that does not occur in the Palearctic region. Owing to the ecological specialization and taxonomic abundance of Cinarine aphids in Neartie America, it seems that the parasite group will be more numerous there, too. Similarly, the Quaternary period's influence is lower due to the retreat possibilities of the tertiary coniferous forest to the south.

In Eurasia, the tertiary coniferous forest centre in eastern Eurasia seems to be the primary original centre of coniferous parasite fauna, too. The species were either distributed in pre-glacial times in Europe, also, but they might have spread here in the Quaternary, due to the existence of a wide taiga coniferous forest belt. Nevertheless, it seems this will be a similar case as in the deciduous forest history. The parasite fauna of the tertiary coniferous forest was separated by the influence of glaciers, some species developing further (vicariants of today), some not—species with the disjunctive recent areas of distribution.

Europe has given origin to the genus *Metaphidius*. This genus is not known from the Far East. For this reason, and also because of the occurrence of separate species of *Pauesia*, we may consider the European Coniferous Forest, better to say their refugia, to be secondary centers of origin of the coniferous forest parasite fauna.

The relation of the northward spread of species of both the ancient complexes mentioned has not been classified as yet due to the poor knowledge of the taiga zone of the USSR.

We may summarize the above as follows: Two ancient faunas—connected either with deciduous or coniferous forest—may basically be recognized. Since the end of the Tertiary and during the Quaternary they have given rise to the various faunas.

The centers of origin are not of the same historic value, the following being recognized: Far Eastern Deciduous Forest, European Deciduous Forest, North American Deciduous Forest, Far Eastern Coniferous Forest, European Coniferous

Forest. From these centers of origin the fauna spread and a part of this fauna has given rise to the rain forest, steppe, desert, forest-tundra fauna of today.

— *Center of distribution.* Because of our comparatively poor knowledge of the distribution and ecology of separate species of parasites, we have to identify today their center of distribution in accordance with their host specificity and distribution. In accordance with the knowledge of the main faunistic complexes, we can classify the species as a member of a certain faunistic complex, i.e. its probable center of origin. Then the host specificity and habitat preference are classified. Further localities and host-specificity in other districts of distribution area are classified from this viewpoint.

In some cases, two of which are mentioned below, the origin is clear and the distribution is restricted to a certain part of Eurasia, the western and eastern parts being clearly separated by the existence of other species in both the districts mentioned.

Examples: *Lysiphlebus ambiguus* is a typical inhabitant of the European Deciduous Forest woodland. Because of its host range it is mostly connected with wet places, neighbourhood of brooks, woody river banks, etc. It spreads, following the mentioned types of habitats, southwards, namely along the rivers. Because of shrubs along the irrigation ditches it occurs commonly in such places in southern Europe, penetrating in this way to the irrigated orchards, gardens and parks, where it may commonly be found elsewhere. The same is true in Asia Minor. The eastward spread reached C. Asia. In the semi-desert and desert zone the species, similarly as in Europe and Asia Minor, is quite common in irrigated places (parks, gardens, fields), but along the irrigating channels, brooks, small rivers, etc. it penetrates far into the real desert and spreads in the neighbourhood, being a parasite of aphids on desert and semi-desert plants. This parasite is able to spread, as is obvious from the mentioned facts, to the south and east in the more xerotherm zones following the humid habitats, although being a member of the European Deciduous Forest complex. Besides, in the south, it attacks new hosts which, however, do not occur in the center of its area of distribution (*Toxoptera aurantii*, *Aphis pumicae*, etc.).

Trioxys angelicae is a typical member of the European Deciduous Forest faunistic complex. Its distribution area, however, covers all Europe including the south, penetrating to Asia Minor. Similarly as *Lysiphlebus ambiguus*, it penetrates into the southern districts following the rivers (woody banks); in the south it occurs in irrigated places (parks, orchards, gardens). Besides the spread into these habitats of the south, it often parasitizes there host aphids that do not occur in C. Europe (*Toxoptera aurantii*).

In the case of a more widely distributed species, in transpalearctic species for example, this is not so obvious. It seems that in some of such cases—e.g. in *Lipolexis gracilis*—the species are Far Eastern as to origin, but they found rather suitable conditions of occurrence in Europe, and such species seem to attack today more species in Europe than they do in the Far East, i.e. in their center of origin. *Ephedrus plagiator*, *E. persicae*, etc., seem to represent similar cases.

Our contemporary knowledge does not allow us to distinguish some subspecies in widely distributed species, although such attempts are known from the literature, these being unjustified in our opinion.

— *Area of distribution.* As in every species, also in the aphidid parasites the area of distribution may be subdivided as follows: (1) Zone of normal distribution, (2) Zone of occasional distribution, (3) Zone of possible (potential) distribution.

The main feature of the zonation in parasite distribution has to be emphasized: The parasites, owing to the main factors determining their distribution, occur today in

certain zones, which are more or less identical with the zonal distribution of separate floras. Nevertheless, because of historical reasons, the parasites usually occur in the normal and occasional zone of distribution, the other habitats of various kinds in other regions having the possibility of being useful, too. The lack of the species in these habitats is due to the place of the center of origin, spreading possibilities, etc. This is of great significance for the biological control (see below).

Horizontal zonation of the area of distribution depends on that of the floristic zones and is shown in many parts of this chapter.

As to the vertical zonation of the area of distribution, the mountain landscapes are typical by their interzonal character. However, the latitudinal belt, in which the mountain ranges are distributed, has a certain influence on the mountains as well. The most peculiar feature of mountains is the vertical zonation.

There is a certain parallelism between the horizontal and vertical zonation. It is conditioned by a decrease in the quantity of heat both in the direction meridian - pole and sea level - upwards. For this reason, there is the same type of distribution of basic zones in dependence on latitude as well as on altitude. Moreover, besides these mentioned similarities, mountain fauna, in general, exhibits its own typical peculiarities.

In accordance with their distribution in various floristic zones, the parasites seem to follow primarily the given floristic zone irrespective of the altitude above sea level. This is true for the temperate climatic belt for example.

In the European mountains, usually the following vertical zonation is developed: Alpine meadows, subalpine meadows, coniferous forest, deciduous forest, steppe (cultivated steppe); the zonation is variable in accordance with the given mountain range, some zones may be absent, etc., but the gradual scheme is the same. Thus, we may find the northern elements to occur in higher altitudes in corresponding zones in C. European mountains, these, however, being present or absent in the lowlands - due to the influence of the Quaternary. For example, *Ephedrus persicae* was found in the deciduous forest upper frontier as a parasite of *Dysaphis sorbi* on *Sorbus* in Δ Triglav, Yugoslavian Alps, near the snow line, in the close neighbourhood of alpine meadows.

Similarly, in the Caucasus, we have ascertained the following vertical zonation in the river Baksan valley up to the peak of Elbrus: 2 - 2,500 m altitude - *Aphis epilobii*, *A. farinosa*, *A. idaei* - members of the deciduous forest zone; *Brachycaudus* sp., *Metopeurum fuscoviride*, *Macrosiphoniella* spp. - ruderal elements of steppe origin. II. About 3,000 m - *Dysaphis* sp., *Brachycaudus* sp., *Aphis fabae* - on subalpine meadows. III. 3,500 m - in the close neighbourhood of a glacier (Terskol and Ink glaciers) - *Betulaphis* sp., *Cavariella* sp., - in forest tundra community. IV. Snow fields, no vegetation. The composition of parasites was basically identical, corresponding to the composition of parasites in the separate latitudinal zones-communities in C. Europe.

A very useful illustrative example may be mentioned: the vertical zonation of aphids in dependence on the flora (NARZYKULOV, 1962), studied in Tajikistan.

1. Semi-savanna or hyperxerophilous open woodlands.

In the lowest localities of river valleys. 300 - 450 m alt.: *Brachycaudus saxaulicae*, *B. calligoni*, *B. plotnikovi*, *B. salsolacearum*, and dominant species characteristic of forest communities of river valleys.

2. Subtropical or arid open woodlands. 500 - 600 m alt. The aphidofauna is richer, due to the richer flora and milder conditions. *Slavum lentiscoides*, *Forda hirsuta* - on *Pistacia* sp.

3. Broadleaved mesophytic deciduous forest. 1100 - 1200 to 2220 - 2400 m alt.

The richest flora and aphid fauna. 70% of aphid species found in Tajikistan occur in this zone. *Anuraphis subterranea*, *Periphyllus mamontovae*, *Dysaphis crataegi*, *Rhopalosiphum* sp., *Hyadaphis* sp., *Chaitophorus* sp., *Betulaphis* sp., *Callipterus* sp., *Chromaphis juglandicola*, *Cavariella* sp., *Cupressobium* sp.

4. Subalpine meadows. 2400 – 2500 to 3,000 – 3200 m alt. No woody plants, poor aphid fauna: *Dysaphis*, *Brachycaudus*, *Capitophorus*, *Nasonovia*, *Acyrtosiphon*.

Unfortunately, no detailed records have been obtained as to the parasites, although the author's studies in 1962 made in the same territories have shown at least the structure of parasite fauna, the composition of which corresponds to the above mentioned vertical zonation also (STARÝ, 1965). Moreover, we have ascertained that the interzonal character of ruderal flora is apparently true for such cases, too, as we have found in C. Asian (Tajikistan) mountains. For example, *Aphidius absinthii*, at about 3000 m alt., this being a species widely distributed in lowland steppes to semidesert zone, from W. Europe to the Far East. However, in the last case, as the zonation in the C. Asian mountains has a different composition on northern and southern slopes, it is also possible that the species had followed, besides the suspected ruderal route, the steppes that reach high altitudes in the mountains as well (southern slopes).

Summarizing, the corresponding floristic zone has to be followed when classifying the vertical zonation influence in the distribution of separate species of parasites in temperate climate districts.

In the tropics, however, the conditions seem to be somewhat different. Primarily, as mentioned above, the aphid parasites do not include originally tropical forms, except for some cases, as to their phylogeny. We must distinguish, too, between the distribution in the tropics and tropical species as to the origin (for example, the tropical cloud forest is generally of a temperate climate, but the tropical rain forest in the lowlands is of a true tropical climate).

In the tropics, too, the features of aphid bionomics and ecology are different. Relative humidity, temperature, shade, presence of host plants, seem to be the main factors determining the occurrence of aphids in the tropics. According to our studies in 1965 in Cuba, a lot of species is rather polyphagous, following their plants from the lowland orchards (originally savanna) to tropical deciduous forest, to lowland type forest, lower mountain rain forest, to cloud forest. Such species (*Toxoptera aurantii*, *Aphis gossypii*, *A. spiraeicola*, *A. craccivora*, etc.) might be mentioned as trans-zonal species in the tropics. The same is true about the parasites of these aphids (*Lysiphlebus testaceipes*). Usually, the mountains in the tropics, due to the perpetual suitable conditions of relative humidity, are the most suitable as to the aphid occurrence, many species being restricted to these places only, although they might be distributed also in the lowlands in case of lack of dry and wet yearly periods.

– *Range of area.* The range of distribution area of a given species is principally dependent on its ecological valence, i.e. on its geological age, which is a rather complicated matter, and the possibilities of spreading over the barriers.

Cosmopolitan species are not common among the parasites, their distribution being the result of human agency in the majority of cases.

Because of the connection of parasites with the separate floras, which are zonal in distribution, the areas of separate groups of parasites were primarily zonal, too, in the frame of a given continent. A number of species that occur in the Palearctic region might be mentioned as examples. But the Quaternary, that had caused such deep changes and migration of different floras, caused also corresponding changes in the distribution of parasites. As a result, the areas of some species are either disjunctive today or (almost) continuous (transpalearctic species).

The small range of area may be either the feature of a group that has not found the

possibility to spread (*Lysiphlebus* spp. in the Far East) or it is a case of an old regressive group. The senescence of a certain group may, however, result in its adaptation on hosts, the ecology of which is somewhat different from the general ecological features; root aphid parasites—*Paralipsis*, *Aclitus*, etc.—seem to be members of very isolated and ancient groups.

— *Stability of area.* Any area of distribution may be:

1. Relatively stable, changing in accordance with time only. This is a case of a strictly specialized species.

2. Unstable, i.e. an area in the process of evolution.

The unstable area is a feature of a species that (a) did not reach the climatic boundaries, (b) is a species in regression, (c) in which changes are caused by the influence of human agency.

Our data are too inadequate owing to the short period of taxonomic knowledge of the group, so that we can hardly speak about a species in regression.

The first case is quite common in a widely specialized species that may attack a new host in the conditions of new environment. For example: previously mentioned cases of European Deciduous Forest species that spread southwards and eastwards. Similarly, the species of Holarctic Forest Tundra seem to spread progressively, too. The third case, the influence of human agency, is also quite common. The accidental introduction of parasites with the host aphid is most common. Nowadays, due to biological control activities, the stability of area of some species has been changed, and further species will be influenced in the future, too.

— *Disjunction of area.* The disjunction of area is usually caused by the following influences:

A. Natural.

1. By the change of climate in a part of the distribution area, where the species is later eradicated. This might be a case of strictly semi-desert species in irrigated lands, of steppe species in case of steppe cultivation, etc.

2. By the migration of plants and their eradication within the limits of the original area. This was a common case in all the Quaternary period, having a corresponding influence on parasite fauna. For example, the disjunction of the tertiary turgian forest had caused the later origin of the European Deciduous Forest and the Far Eastern Deciduous Forest complexes, while some species have occurred in both parts of the original area till now.

3. By the submersion or separation of parts of land. This is a case of separation of Palearctic and Nearctic regions, with a corresponding influence on the fauna of coniferous and deciduous forest.

B. Unnatural, caused by man's agency.

4. Accidental introduction. Several species of parasites (*Diaeretiella rapae*) have been incidentally introduced in the greatest part of the world.

5. Introduction for biological control purpose. Here the generally known transferring of parasites of *Therioaphis trifolii* from the Old World to California and their successful establishment can serve as an example.

— *Area and effectiveness.* There is a general rule known with the natural enemies, that not one species of a natural coenomy complex is likely to be effective throughout the range of its host (FLANDERS, 1959).

We have unfortunately no detailed records on the aphid parasites in this respect. Nevertheless, field observations on practically each species may show that it is more common in one and less common in another habitat, this being also connected with the effectiveness. Detailed records on the relative effectiveness of some parasites have been obtained by American authors in biological control experiments on *Therioaphis*

trifolii, the area dependence of effectiveness being clearly shown by comparison of the parasite effectiveness in different parts of California (see: v.d. BOSCH et al., 1964). These detailed observations have obviously shown the variability of degree of effectiveness on the conditions of the environment, in spite of the environment being somewhat unnatural for the introduced species. Nevertheless, we have no really detailed records from the whole area of a parasite species to show exactly the degree of effectiveness-dependence on the area. We can believe only that it varies in a similar way as in the smaller districts, from where the records are obtainable in the literature.

— *Vicariants*. Systematical vicariants. A splendid example of a big group of systematical vicariants may be mentioned if the Far Eastern Deciduous and European Deciduous Forest complexes are compared. Due to the disjunction of areas of species of the tertiary turgai forest in the Quaternary, in a number of cases the separated populations have given origin to separate species:

Far Eastern Deciduous Forest

Aclitus sp. (SHIGA, in litt.)

Aphidius areolatus

Praon orientale

Protaphidius nawaii

Toxares shigai

(*Paralipsis eikoe*)

European Deciduous Forest

Aclitus obscuripennis

Aphidius setiger

Praon volucre

Protaphidius wissmannii

Toxares deltiger

(*Paralipsis eucervis*)

Ecological vicariants. Many species related ecologically but not systematically might be mentioned.

— *Endemics*. The parasite species in a given area might be:

A. Autochthonous, if they originated in situ. This is the case of the Far Eastern Deciduous Forest complex, that originated at the very place at the Tertiary, or it is the remains of typical fauna that was widely distributed in the turgai forest type in the Tertiary.

B. Allochthonous, if they are immigrants from the neighbouring area.

As it is known, the criterion of endemism is relative in a certain degree, as it changes in dependence on time. This is just the case of the aphidiid parasites, the distribution of which depends on the distribution and migrations of certain floras. For this reason, it would be better in our opinion to classify certain species as endemics of a certain floristic zone or flora than as endemics of a certain continent or country. If this criterion is accepted, endemism is quite a common matter among the aphidiids, corresponding to the phylogeny of the group in accordance with the evolution of floras and fauna of hosts.

Our viewpoint may be illustrated by the following rather typical example—*Monoctonia pistaciaecola*. It was described originally as a parasite of the leaf-curling aphid *Forda* sp., on *Pistacia* sp. from the Crimea, U.S.S.R. Phylogenetically, it is no doubt a very peculiar and isolated group. Later, it was found to occur in Tertiary relic *Pistacia* forests in the C. Asian mountains, the U.S.S.R., as a parasite of *Forda*-aphids. But, in similar habitats, it was found to occur as a parasite of gall-aphids *Pemphigus* sp. on *Populus*. Later, it was found as a parasite of *Forda* sp. on *Pistacia* sp. in southern Italy. There is no doubt, if the species would be primarily found to occur as a parasite of *Forda* sp. in the mentioned Tertiary relic *Pistacia* forest in C. Asian mountains, it would be quite probable that the commonly used criterion "endemic of Central Asia" would be applied, too, in this case. Nevertheless, our recent classification keeps *M. pistaciaecola* as a member of the Mediterranean faunistic complex, which also reaches C. Asia and C. Europe. We may expect the species will be found in other parts of the Mediterranean, too. Ecologically, it is a parasite of certain gall aphids (*Forda*, *Pemphigus*). It is a typical inhabitant of the Mediterranean-type

districts, nevertheless, it occurs in the C. Asian Deciduous Forest, with the same or very similar host complex, while in C. Europe it attacks only *Pemphigus*-species as *Forda*-aphids occur here exclusively as anholocyclic species (root aphids), their primary host plant—*Pistacia*—being absent in C. Europe.

—*Relics*. Tertiary relics. The species of the recent Far Eastern Deciduous Forest complex may be mostly classified as tertiary relics as we know that both floristic and faunistic records show the conditions of environment have almost not changed in this territory since the Tertiary.

In other cases it seems unjustified to classify the species of separate faunistic complexes as relics, as due to the migration of floras, parasite complexes had also changed their areas. The incidental occurrence of a species in a place far from its known distribution area is apparently mostly due to the incidental immigration (air streams) than to the relic character.

A case of *Trioxys pannonicus*, which is a member of the Eurasian Steppes faunistic complex, and was found as the supposed Tertiary relic in the Canary Islands (MACRAUER, 1962) has to be classified from the mentioned point of view as well. The details are presented in the chapter on Island parasite fauna.

—HOST SPECIFICITY OF PARASITES is influenced by a great number of factors, dealt with earlier in more detail (see: Host specificity). Our observations have shown that the habitat is of greatest significance. The influence of habitat is most remarkable in the temperate climate zone, having certain other apparently derived features in the tropics. In parasites of the monoecious aphid species the importance of relation to the habitat is less distinct as these parasites occur mostly, similarly as their hosts, throughout all the season in the same type of habitat (forest, steppe). The relation to the habitat is more apparent in parasites of dioecious aphids because of the migration from primary to secondary host plants, change the type of habitat (Forest-steppe-forest). In this case a dioecious aphid species is attacked by different complexes of parasites the composition of which depends on the type of habitat in which they occur. As far as it is known, dioecious aphid parasites do not include the monophagous species; after emigration of a dioecious aphid host the parasites infest other aphid species, either other dioecious aphids still occurring in the habitat, or some other suitable monoecious species. In other cases dioecious aphid parasites enter diapause during this time. The importance of the habitat is also recognizable from the fact that the type of habitat is more important than the presence of primary or secondary host plants. In case of a certain intermediary habitat, where primary and secondary host plants (shrubs and herbs) occur together, the parasite complex corresponds to the given type of habitat or may be mixed.

The existence of a suitable host in a suitable type of habitat is a further prerequisite for the parasite existence. The host suitability is determined on the one hand by the phylogenetical relationship of the host and the parasite, on the other hand by the range of plasticity of parasite specificity. These two factors are of a different degree of importance, their influence being changed during the phylogeny. Both clear cases of a strict adaptation of an aphid parasite to its host, and cases where the mode of host life is more important than host-parasite phylogenetical relationship, and a number of intermediary cases, are known. Although floristic zone dependence of parasites seems to be satisfactorily proved, there is no doubt that a lot of intermediary zones occur, where the parasites attached to both neighbouring zones may be found, or some species may penetrate from one zone into another.

The strictly specialized ("monophagous") parasites are restricted to a single host species, their specificity cannot vary in various parts of their distribution area, although their distribution area may not be identical with that of the host.

In less and widely specialized parasite species the following cases are known to occur:

A. Distribution area of the parasite is wider than that of its host. Example: *Aphidius absinthii* is a European steppe element, distributed from western Europe to the Far East. It is restricted as to the host range to *Macrosiphoniella* species, attacking various species of this genus all over its distribution area.

B. Distribution area of the parasite is approximately equal to that of the host species. Example: This is a common case in a number of less specialized parasites that attack several host aphids or aphid groups and occur in more or less the same conditions. Both the host aphids and parasites are mostly represented by a not too progressive species that are closely connected with a certain type of habitat (European Deciduous Forest, etc.).

C. Distribution area of the parasite is smaller than that of the host aphid.

(a) The smaller distribution area of the parasite is due to the influence of geological history and less ability of the parasite to spread. Example: Some *Periphyllus* species are distributed all over the Palearctic region. They are attacked by two groups of closely related parasite species that represent systematic vicariants due to the history of the tertiary deciduous forest: *Aphidius setiger* in Europe, *A. areolatus* in the Far East.

(b) The smaller distribution area of the parasite is due to the influence of geological history and lower ability of the parasite to spread because of certain close connections with temperature conditions. Example: *Aphidius transcaspicus*, though widely distributed from the Mediterranean to C. Asia, attacks one of its host species, *Hyalopterus pruni*, in this area only, while the host aphid is much more distributed, e.g. northward, not being followed to these districts by the parasite.

It is possible that the host specificity patterns will vary in accordance with the centers of distribution, between Eurasia and Nearctic America namely. The Nearctic aphids often seem to exhibit a combination of host plants, that is quite unusual for similar conditions of Europe (Dr. HOLMAN, personal communication); the same might be true as to the parasites, nevertheless, the known records do not seem to permit any generalization as yet.

This relation of host preference of parasites and geographic distribution is obvious in a widely specialized parasite species:

According to our observations the host preference of parasites is different in various parts of their distribution area. The widely distributed species naturally fall under the influence of other environments. In these other environments they come into contact with other hosts—either other species of the same genus in case of more strictly specialized parasites, or species of other aphid groups that are more or less phylogenetically or ecologically related. Because of their host range they are able to attack such hosts and successfully parasitize them or not. If the main host or host groups "A" is scarce or absent in the new environment, the parasite adapts to other hosts which may either be entirely new for it or they may be alternative or additional hosts in the area of the main host "A". These hosts then become main hosts "B" of the parasite in other given areas. Two examples of a somewhat different kind might be mentioned:

Ephedrus persicae. In Europe distinctly prefers members of the Anuraphidine and Myzine aphids, leaf-curling species for example, in Asia Minor it attacks many Aphidine and Myzine aphids. No doubt, the host preference is apparently influenced by the occurrence in different habitats that is connected with the southward distribution of the parasite. In the Far East, it mostly attacks the freely living and leaf-curling aphids of the Aphidine and Myzine groups, and reproduces parthenogenet-

ically there. Its host range in the Nearctic America covers also such species which are not parasitized in Europe, being present or not in this area.

Diaeretiella rapae in Europe attacks mostly *Brevicoryne brassicae*, *Hayhurstia atriplicis*, *Myzus persicae*, and some other aphid groups rarely. The host preference is different in various parts of Europe. In Nearctic America, it is known as a parasite of some *Aphis*-species, too.

Lysiphlebus ambiguus and *Trioxys angelicae* can also be mentioned. Their host range in southern Europe differs from that of C. Europe, as they infest in the south species that do not occur in C. Europe.

The different host preference seems to be an indication of the possible existence of biological races, etc. in separate species, nevertheless, our knowledge is too inadequate to establish some clear cases based not only on field but also on experimental observations and studies.

Faunistic Complexes

The distribution and occurrence of the parasites of nowadays shows that the group has been primarily connected with the typical North-South zonation of plant communities. Nevertheless, the original zonation belts were deeply influenced by glacial periods, the original distribution areas of parasites being changed, separated into several parts, put under influences of different climates, etc. This has resulted in the existence of certain groups of parasites in various areas, the separate groups often having a different origin—the faunistic complexes of more or less recent types have originated.

The faunistic complexes of today, as mentioned above, are partially the more or less original complexes of the late Tertiary; the others have changed due to the migration of floras and faunas in the Quaternary. It has to be stressed that the ancient faunistic complexes originated in separate floristic zones, after the disjunction of these zones because of continental changes, climatic changes, etc., later they differentiated in separate continents, their original connection being, however, obvious also at the present time if the historical factors are evaluated.

Our maps, being made in accordance with the corresponding level of our knowledge, will no doubt change somewhat after further records are obtained, nevertheless, the main ideas on the geographic distribution of parasites seem to be usefully illustrated.

— A review

— *Holarctic Forest Tundra* (Fig. 273). Characteristics: It is typical for cool arctic climate conditions, being a transitional zone between forest-free tundra area in the north and mostly coniferous taiga forests in the south. It covers both the forest-tundra where the forests occur in river valleys and protected places, and open woodland. The following trees are usually mentioned as typical: *Salix*, *Alnus*, *Betula*, etc. Distribution: The forest tundra sub-zone is holarctic, circumpolar in distribution. The tundra zone is situated between the arctic rock deserts and coniferous or boreal forests. Due to the influence of the Quaternary, many elements of the forest-tundra may be found far in the south, in parks and at higher altitudes in the mountains, or in the lowlands (peat bogs). Typical species: *Aphidius cingulatus*: distribution: Europe, Ireland, Kazakhstan — U.S.S.R., Iceland, U.S.A. — Mass., D.C., Ohio, Calif.; host range *Pterocomma* spp. on *Salix*, *Populus*. *Lysiphlebus salicaphis*: Europe, C. Asia, S. Korea, U.S.A. — N.Y., Ohio, Colo., Utah, California, Wash., Sask.; *Chaitophorus* spp. on *Salix*, *Populus*. *Aphidius sicarius*: Germany, Czechoslovakia, Finland,

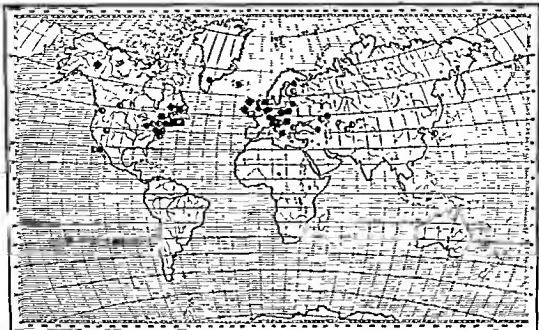


Fig. 273. Faunistic complexes of parasites - Holarctic Forest Tundra. ● *Aphidius cingulatus*, ○ *Lysiphlebus salicaphis*, ■ *Trioxya betulae*, ◆ *Tr. compressicornis*, ◻ *T. ibis*.

U.S.S.R. - Latvia, Siberia; *Betulaphis*, *Calaphis*, on *Betula*. *Ephedrus brevis*: Br. Isles, Czechoslovakia, probably northern parts of N. America as well. *Trioxya betulae*: C. Europe, N. Europe, Br. Isles, eastern N. America, *Betarallia*, *Symydobius*, *Kal-listaphis*, etc. on *Betula*. *Trioxya compressicornis*: C. and N. Europe, Br. Isles, Iceland, N. America; *Euceraphis* spp. on *Betula*. *Trioxya ibis*: Br. Isles, eastern N. America, *Betulaphis* sp. on *Betula*. Origin: The origin of this complex is probably in the post-glacial periods. It seems to be the youngest complex of parasites of any. Relations: Due to the taxonomic relations of the species of this complex it is connected with the European Deciduous Forest. Certain members of this complex were often to be found in deciduous forest habitats, but they also penetrate into the steppe and semi-desert zone (river-valleys). Similarly, they may be found in corresponding communities of forest-tundra types in Europe and the Caucasus.

- *Boreal Europe* (Fig. 274). Characteristics: It is typical for cooler climatic conditions. Because of its origin, it is probably closely connected with forest-tundra zone. Distribution: It is restricted to the northern parts of Europe, separate species being distributed in various degrees to the south in a similar way as in forest-tundra elements. Because of its transitional character, elements of this complex may be found, besides the forest-tundra, also in mountain and submountain forest undergrowth. Typical species: *Diaeretellus ephippium*: Br. Isles, Germany, Czechoslovakia, Sweden; *Decorosiphon* sp. on mosses. *Diaeretellus heinzei*: Czechoslovakia, Germany, Sweden; aphids on mosses. *Diaeretellus macrocarpus*: Germany, Czechoslovakia; Saltusaphidine aphids. *Diaeretellus palustris*: Germany; *Rhopalosiphum nymphaeae* on secondary host plants. *Praon necans*: Germany, Czechoslovakia; *Rhopalosiphum nymphaeae* on secondary host plants. Origin: It is a very young complex, probably of post-glacial periods. Relations: It is closely associated with the forest tundra, being typical for peat bogs and allied habitats. It often occurs in the same places as members of the Forest-tundra faunistic complex. Nevertheless, due to the host range of different members



Fig. 274. Faunistic complexes of parasites – Boreal Europe. ● *Diacretellus ephippium*, ○ *D. helizet*, ◐ *D. macrocarpus*, ⊗ *D. palustris*.

that are connected with aphids of low spread possibilities, it is believed its members were unable to spread to North America.

– *West Eurasian Coniferous Forest* (Fig. 275). Characteristics: It is typical for coniferous and mixed forests of Europe. Distribution: Members of this complex are distributed almost all over Europe, from the north to the south, penetrating to the Mediterranean. Typical species: *Metaphidius aterrimus*; Austria, Germany, Czechoslovakia; *Cinara* spp. on conifers. *Pauesia alpina*: Italy (Alps); *Cinara* spp. – conifers. *Pauesia cupressobii*: Czechoslovakia; *Cupressobium* spp. – conifers (Juniperus). *Pauesia goidanichi*: Italy (north); *Cupressobium* spp. – conifers (Juniperus). *Pauesia grossa*: Austria, Czechoslovakia; *Todolachnus* spp. conifers. *Pauesia juniperorum*: Czechoslovakia, *Cupressobium* spp. – conifers (Juniperus). *Pauesia media*: Italy (north); *Cupressobium* spp. – conifers (Juniperus). *Pauesia montana*: Italy (north); *Todolachnus* spp. – conifers. *Pauesia piceacollis*: Germany, Czechoslovakia, USSR-Lithuania; *Cinara* spp. – conifers. *Pauesia picta*: Germany, Sweden, Austria, Br. Isles, Bulgaria; *Cinara* spp. – conifers. *Pauesia pinicollis*: Germany; *Cinara* spp. – conifers. *Pauesia rufiabdominalis*: Italy, *Cinara* spp. – conifers. *Pauesia silvestris*: Italy, Czechoslovakia; *Cinara* spp. – conifers. *Pauesia similis*: Italy (north); *Cinara* spp. – conifers. The following two species are secondary elements, being primarily members of deciduous forest type communities: *Lysaphidius schimitscheki*: Germany; *Liosomaphis abietina* – Abies. *Praon bicolor*: Germany, Czechoslovakia; *Protolachnus* spp. – conifers. Origin: It seems to be a derived complex, the Far Eastern coniferous forest being its source. Its formation had begun probably in the coniferous forests refugia in Europe during the Quaternary. Rela-



Fig. 275. Faunistic complexes of parasites - West-Eurasian Coniferous Forest. ● *Lysaphidus schimitscheki*, ○ *Metaphidius aterrimus*, ⊕ *Praon bicolor*, ⊙ *Pauesia alpina*, ⊖ *P. cypressobii*, ⊗ *P. goidanichii*, ⊕ *P. grossa*, ⊙ *P. montana*, ⊖ *P. picta*.

tions: This complex has obvious and strong connections with the East Eurasian Coniferous forest complex. Its northeastern limits are unknown because of insufficient knowledge of taiga coniferous forest territories. The two species *Lysaphidus schimitscheki* and *Praon bicolor* are no doubt elements of deciduous forests that penetrated into the coniferous forests and successfully adapted there. They infest either the hosts of similar origin (*L. schimitscheki*), or they attack the typical coniferous forests aphid species (*P. bicolor*).

- East Eurasian Coniferous Forest (Fig. 276). Characteristics: It is typical for the Far Eastern type of coniferous forest. Distribution: It has been primarily distributed all over coniferous forest belts in the Tertiary, the disjunction being of Quaternary origin. Some species of the complex are widely distributed in Europe, too, their areas of distribution being either disjuncted or they may be almost continuous but poorly known. Some species penetrate also into Africa (incidental introduction?). Typical species: *Diaeretus leukopterus*: Europe, Japan, S. Korea; *Protolachnus* spp. - conifers. *Pauesia abietis*: Europe, Asia M., Japan; *Cinara* spp. - conifers. *Pauesia infulata*: Europe, Far East; *Cinara*, *Buchneria*, *Cupressobium* spp. - conifers. *Pauesia inonyei*: Far East; *Cinara* spp. - conifers. *Pauesia jezoensis*: Europe, Far East, *Cinara* spp. - conifers. *Pauesia konoi*: Far East; *Cinara* spp. - conifers. *Pauesia laricis*: Europe, Far East; *Cinara* spp. - conifers. *Pauesia momicola*: Far East; *Cinara* spp. - conifers. *Pauesia nopporensis*: Far East; *Cinara* spp. - conifers. *Pauesia pini*: Europe, Far East; *Cinara* spp. - conifers. *Pauesia soranumensis*: Far East; *Cinara* spp. - conifers. *Pauesia unilachni*: Europe, Far East, Aethiop. (Congo ex-Belge), *Schizolachnus* spp. - conifers. Origin: The origin of this complex is of Tertiary age, in the coniferous forest belt. Relations: It is widely distributed and has also close connections with West Eurasian Coniferous Forest complex.

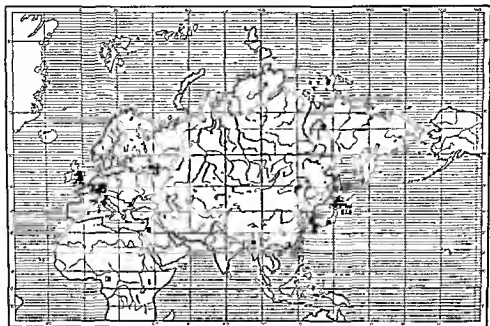


Fig. 276. Faunistic complexes of parasites-East-Eurasian Coniferous Forest. ■ *Diaeretus lincopertus*, ▣ *Pauesia abitis*, ▤ *P. infusata*, ▥ *P. mouyei*, ▦ *P. kouoi*, ▧ *P. laricis*, ▨ *P. nopporomensis*, ▩ *P. pini*, □ *P. unilachui*.

– **North American Coniferous Forest.** Characteristics: It is typical for the coniferous forest of Nearctic America. Distribution: Similarly as the other complexes, we have left all the Nearctic complexes unclassified in a more detailed way as we had no opportunity either to stay and use our research methods in this area, or to examine sufficient material. Typical species: *Pauesia bicolor*: N.J. to Fla., Ohio, Wis.; *Cinara* spp. – conifers. *Pauesia californica*: Calif., S. Dak., Ohio, Brit. Columbia; *Schizolachnus* spp. and allied genera – conifers. *Pauesia gillettei*: Colo., La.; *Cinara* spp. – conifers. *Pauesia juniperaphidis*: Ohio, Colo., Idaho; *Cinara* spp. – conifers. *Pauesia nigrovaria*: Calif.; *Cinara* spp. – conifers. *Pauesia ponderosae*: Brit. Columbia; *Cinara* spp. – conifers. *Pauesia prociphali*: D.C., Va., N.C., Minn., Wash.; *Cinara* spp. – conifers. *Pauesia scorpinea*: Va. *Pauesia takomaensis*: Md., Va., Colo.; *Cinara* spp., conifers. *Pauesia varigata*: Colo.; *Cinara* spp. – conifers. *Pauesia xanthothera*: N.C., Va.; *Cinara* spp. – conifers. *Xenostigmus bifasciatus*: N.C., Md., Fla., Utah, Nebr., Wash.; *Cinara* spp. – conifers. Origin: Because of the retreat and remigration possibilities of the Tertiary coniferous forest in the Quaternary, it seems that this coniferous forest complex has originated in the Tertiary. Relations: due to the generic composition of parasites and history of coniferous floras of the Holarctics, it is evolutionarily related to the East Eurasian complex, present relations being probably none.

– **European Deciduous Forest (Fig. 277).** Characteristics: It is typical for the deciduous forests of Europe. Distribution: All the species are mostly restricted to Europe in distribution, some of them penetrating, however, to Asia Minor and rarely to C. Asia, following the deciduous forest elements. Typical species: *Achitus obscuripennis*: Germany, Czechoslovakia; *Anoeia* spp. and probably other root aphids. *Aphidius caraganae*: Europe; *Acyrtosiphon caraganae* – Caragana. *Aphidius hieraciorum*: Europe. *Nasonovia* spp. *Aphidius hortensis*: Europe, Nea. (accid. intr.): *Liosomaphys berberidis* – Berberis. *Aphidius loncerae*: Europe; *Amphorophora*, *Macro-*

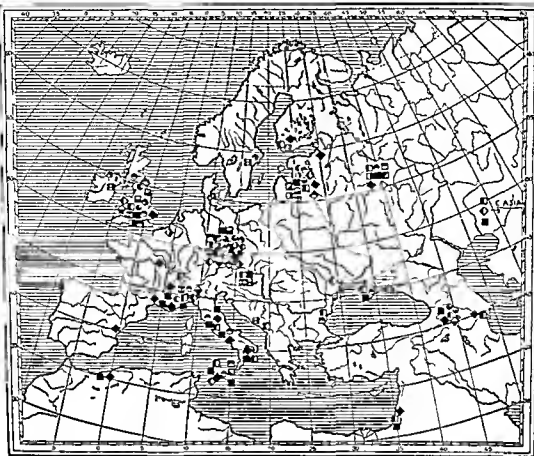


Fig. 277. Faunistic complexes of parasites – European Deciduous Forest. ● *Achilus obscuripennis*, ○ *Aphidius hortensis*, ○ *A. lonicerae*, ○ *A. rosae*, ○ *A. setiger*, ● *Areopraon lepelleyi*, ● *Dyscritulus planiceps*, ● *Ephedrus cerasicola*, ● *E. minor*, ■ *Lysiphlebus ambiguus*, ■ *L. thelaxis*, ■ *Monoctonus crepidis*, ■ *M. pseudoplatani*, ■ *Praon abjectum*, ■ *Pr. flavinode*, ■ *Pr. volucre*, ■ *Protaphidius wissmannii*, ■ *Toxares deltiger*, ◆ *Trioxys angelicae*, ◆ *Tr. cirsi*, ◆ *Tr. falcatus*, ◆ *Tr. pallidus*, ◆ *Tr. phyllaphidis*.

siphum, etc. *Aphidius megourae*: Europe; *Megoura viciae*. *Aphidius nigrescens*: Europe; *Aulacorthum* spp. *Aphidius ribis*; *Cryptomyzus* spp. and rel. groups. *Aphidius rosae*: Europe, Nea. (accid. introd.); *Macrosiphum* etc. *Aphidius rubi*: Europe; *Macrosiphum*, *Nectarosiphum*. *Aphidius setiger*: Europe, Caucasus; *Periphyllus* spp. *Areopraon lepelleyi*: Europe, *Schizoneura* spp. – galls. *Dyscritulus planiceps*: Europe; *Drepanosiphum* spp. – *Acer*. *Ephedrus cerasicola*: Europe; *Myzus cerasi* – *Prunus*. *Ephedrus minor*: Europe; *Myzaphidine* and *Liosomaphidine* aphids (*Myzaphis*, *Cavariella*, *Passerina*). *Lysiphlebus ambiguus*: Europe, Caucasus, C. Asia; *Aphis*, *Brachycaudus*, etc. *Lysiphlebus dissolutus*: Europe; *Asioecia* spp. – roots. *Lysiphlebus thelaxis*: Europe (prob. south to C.); *Thelaxes* spp. – *Quercus*. *Monoctonus angustivalvus*: Europe; *Nasonovia* spp. *Monoctonus caricis*: Europe; *Metopolophium*, *Sitobium*, etc. *Monoctonus cerasi*: Europe, leaf curling aphids (*Aphis*, *Dysaphis*, *Myzus*, etc.). *Monoctonus crepidis*: Europe, Canada (accid. introd.); *Nasonovia* spp., etc. *Monoctonus nervosus*: Europe, C. Asia; *Impatiens* spp. *Monoctonus pseudoplatani*: Europe; *Drepanosiphum* spp. *Pauesia maculolachni*: Europe; *Maculolachnus* spp. – *Rosa*. Note: This is primarily a member of a coniferous forest. *Praon abjectum*: Europe; *Aphis* spp. *Praon flavinode*: Europe. Arborescent callaphidid species. *Praon grossum*: Europe; *Amphorophora* spp. *Praon pubescens*



Fig. 278. Faunistic complexes of parasites - Far Eastern Deciduous Forest. ● *Aclitus* sp., ● *Aphidius arcolatus*, ● *A. salignae*, ● *A. salicis*, ○ *Ephedrus lacertosus*, ○ *E. persicae*, ○ *E. plagiator*, ○ *E. validus*, ■ *Lysiphbia japonica*, ■ *L. rugosa*, ■ *Monoclonus similis*, ■ *M. woodwardiae*, ■ *Paralipsis eikoae*, ■ *Panesia japonica* ◆ *Praon orientale*, ● *Protaphidius nawai*, ◆ *Toxares shigai*, ◆ *Trioxys luteolus*, ◆ *Tr. ornatalis*.

Europe, *Nasonovia* spp. *Praon rosaeicola*: Europe; *Macrosiphum rosae* - *Rosa* spp. *Praon silvestre*: Europe; *Periphyllus* spp. - *Acer*. *Praon volucre*: Europe, Asia M., Caucasus, C. Asia; *Acyrtosiphon*, *Brachycandus*, *Hyalopterus*, *Hyperomyzus*, *Macrosiphum*, *Myzus*, *Sitobium*, etc. *Protaphidius wissmannii*: Europe, *Stomaphis* spp. Note: This is primarily a member of coniferous forest. *Toxares deltiger*: Europe; Forest inhabiting aphids (*Acyrtosiphon*, etc.). *Trioxys angelicae*: Europe, Asia M.; Aphidine aphids, etc. *Trioxys heraclei*: Europe, *Cavariella* spp. etc. *Trioxys letifer*: Europe; *Cavariella* sp. *Trioxys cirsii*: Europe; *Drepanosiphum* spp. *Trioxys falcatus*: Europe, Caucasus; *Periphyllus* spp. *Trioxys hortorum*: Europe; *Timocallis* spp. *Trioxys pallidus*: Europe, C. Asia, Callaphidid arboricolous species. *Trioxys phyllaphidis*: Europe, *Phyllaphis* sp. Origin: The origin of this complex is clearly in the Tertiary deciduous forest belt. The separation and further development of this complex has been due to the influence of the Quaternary. Relations: Strong connections with the Far Eastern Deciduous forest still occur, being recognizable from the occurrence of their identical species, or of systematically vicariant species. Some species penetrate to the north (holartic forest tundra).

- Far Eastern Deciduous Forest (Fig. 278). Characteristics: It is typical of the Far Eastern Deciduous forest type. Distribution: It is distributed in the Far East, penetrating to the allied tropics, or on the other hand, some elements have a wide transpalearctic distribution, following the deciduous forest elements, their areas being either disjunctive or almost continuous. Typical species: *Aclitus* sp. (SINGA, in litt.): Far East, *Sappaphis* spp. - roots. *Aphidius arcolatus*: Far East; *Periphyllus* spp. - *Acer*. *Aphidius* gr. *gifuensis*: Far East, *Macrosiphum*, *Myzus*, *Acyrtosiphon*, etc. *Aphidius salignae*: Far East; *Tuberolachnus salignus* - *Salix*. *Aphidius salicis*: Europe, Far East.

Cavariella spp. etc. *Ephedrus lacertosus*: Europe, Far East; *Macrosiphum*, *Myzus*, *Nectarosiphum*, *Rhopalosiphoninus*. *Ephedrus persicae*: Europe, C. Asia, Asia M., Far East, Nea., Australia; Anuraphidine, Myzine, Aphidine aphids, etc. (galls, leaf-curling namely). *Ephedrus plagiator*: Europe, Far East; Aphidine, Myzine aphids (mostly leaf-curling). *Ephedrus validus*: Europe, Far East; Eriosomatine aphids. *Lysiphlebia japonica*: Far East. Aphidine aphids, etc. *Lysiphlebia rugosa*: Far East; Aphidine aphids. *Monoctonus similis*: Far East; *Myzus* sp. *Monoctonus watanabei*: Far East; *Mansakia shirabae* - *Betula*. *Monoctonus woodwardiae*: Far East; *Myzus* sp. *Paralipsis eikoe*: Far East; Host range unknown. *Panesia japonica*: Far East; *Lachnus tropicalis* - *Quercus*, *Castanea*. This is primarily a member of a coniferous forest complex. *Panesia tropicalis*: Far East; *Lachnus* sp. - *Ficus*. Note: Member of a coniferous complex. *Praon glabrum*: Far East; *Euceraflis* spp. - *Betula*. *Praon orientale*: Far East; Myzine etc. aphids (*Macrosiphum*, *Aphis*, *Acyrtosiphon*). *Protaphidius naivaii*: Far East; *Stomaphis* spp. Note: Primarily a member of a coniferous forest complex. *Toxares shigai*: Far East; Host specificity unknown. *Trioxys brunneus*: Far East; *Acyrtosiphon* spp. *Trioxys carinatus*: Far East; *Macrosiphum* spp. *Trioxys luteolus*: Far East; *Shiraphis*, etc. - *Acacia*. *Trioxys orientalis*: Far East; *Macrosiphum* spp. Origin: The origin of this complex is of Tertiary period. Relations: It has strong relations to its derivate—European Deciduous Forest complex; a number of vicariant or identical species occur.

- *Mediterranean*. (Fig. 279). Characteristics: It is typical of the forest-steppe areas of the Mediterranean. Distribution: It is restricted to the xerothermic type of the Mediterranean climate, penetrating partly into Europe and eastward to C. Asian steppes and semi-deserts following the type of climate and corresponding flora. Typical species: *Aphidius transcaspicus*: S. Europe, Asia M., C. Asia; *Hyalopterus*, *Longinervis*. *Monoctonia pistaciaecola*: C. Europe, S. Italy, Crimea - USSR, C. Asia - USSR; *Forda* spp. - *Pistacia*, *Pemphigus* spp. - *Populus* (galls). Origin: The complex seems to have originated in the Tertiary. Relations: It seems to be an isolated complex.

- *North American Deciduous forest*. Characteristics: Typical of deciduous forest zone of Nearctic America. Distribution: No more detailed research has been made (see above). It penetrates probably into other Nearctic zones as in the case of the European Forest complex. Typical species: *Praon nebulosus*; Iowa, Colo. - *Periphyllus* spp. *Trioxys antaeus*: Ohio, Md., Fla; *Drepanaphis* spp. Note: Only two species have been mentioned, the complex being believed to be much more numerous. Origin: Because of the history of the deciduous forest belt, it seems there are some ancient original connections with the Far Eastern deciduous forest type. Some species might be systematical or ecological vicariants. Further research is necessary. Relations: The present relations are unknown.

- *Eurasian Steppes*. (Fig. 280). Characteristics: It is a very typical complex of the Eurasian steppe type areas. Distribution: It is widely distributed, following the steppe zone of Eurasia. Nevertheless, due to the cultivation of forest and originating of the so called cultivated steppe landscape, it has penetrated almost all over the lowland and submountain parts of Europe. Further, it has spread east- and southward to the semi-desert zone, some species reaching the Far East. Typical species: *Aphidius absinthii*: Europe, C. Asia, Far East; *Macrosiphonella* spp. *Aphidius avenae*: Europe, Far East; *Sitobium* spp. *Aphidius ervi*: Pal., Nea., Orient. *Acyrtosiphon* spp., *Microlophium*. *Aphidius fumebris*: Europe, N. Africa; *Dactynotus* spp. *Aphidius matricariae*: Pal., Nea., etc.; Aphidine, Myzine, etc. aphids. *Aphidius mitorarsi*: Europe; *Mitorarsi* spp. *Aphidius pascuorum*: Europe; *Sitobium*, *Metopolophium*, etc. - grasses. *Aphidius phalaugomyzi*: Europe; *Phalangomyzus* spp. *Aphidius picipes*: Europe. Myzine



Fig. 279. Faunistic complexes of parasites – Mediterranean. ● *Aphidius transeaspicus*, ○ Ditto, introduced, ● *Monoctonia pistaciaecola*.



Fig. 280. Faunistic complexes of parasites – Eurasian Steppes. ■ *Aphidius absinthii*, □ *A. avenae*, ▲ *A. ervi*, □ *A. funebris*, □ *Ephedrus campestris*, ◆ *Lipolexis gracilis*, ◇ *Lysiphlebus fabarum*, ◇ *Parapsis enervis*, ● *Praon exoletum*, ○ *Trioxys aculephac*, ○ *Tr. panonicus*. – Central Asia Deserts. ● *Trioxys asiaticus*, ■ *Lysiphlebus desertorum*.

aphids. *Aphidius sonchi*: Europe; *Hyperomyzus* spp. *Aphidius tanacetarius*: Europe; *Metopeurum* spp. - *Tanacetum*. *Ephedrus campestris*: Europe, Far East; *Macrosiphoniella*, *Dactynotus*, *Megoura*. *Ephedrus nachei*: Europe; *Cryptosiphum*, *Hayhurstia* (leaf-curling, galls). *Lipolexis gracilis*: Europe, Far East; *Aphis*, *Brachycaudus*, *Myzine* aphids, etc. *Lysaphidus arvensis*: Europe; *Colorado* spp. *Lysaphidus erysimi*: Europe; *Lipaphis*, *Pseudobrevicoryne*. *Lysiphlebus arvicola*: Europe, C. Asia; *Siphia* spp. *Lysiphlebus fabarum*: Europe, Asia M., Caucasus, C. Asia; *Aphis*, *Brachycaudus*, etc. *Lysiphlebus fritzuelleri*: Europe, Siberia; *Aphis tracciae*. *Lysiphlebus hirticornis*: Europe; *Metopeurum* spp. - *Tanacetum*. *Lysiphlebus melandriicola*: Europe; *Brachycaudus* spp. - *Melandrium*. *Paralipsis euervis*: Europe; Root aphids. *Praon absinthii*: Europe; *Macrosiphoniella*, *Titanosiphon*. *Praon dorsale*: Europe, C. Asia; *Dactynotus*, *Acyrtosiphon*. *Praon exoletum*: Europe, N. Africa, Asia M., C. Asia, Nea. (introduced); *Therioaphis* spp. *Trioxys aculephae*: Europe, Far East; *Aphis* spp. *Trioxys brevicornis*: Europe; *Cavariella*, *Hyadaphis*, *Staegeriella*, etc. *Trioxys centaurae*: Europe; *Dactynotus*, *Macrosiphoniella*. *Trioxys complanatus*: S. Europe, Asia M., N. Africa, C. Asia, Nea. (introduced); *Therioaphis* spp. *Trioxys genistae*: Europe; *Aphis genistae*. *Trioxys glaber*: Europe; *Aphis gallii-scabri*. *Trioxys paumotuensis*: Europe, Canary Isl.; *Titanosiphon*. *Trioxys parauctus*: Europe; *Hyadaphis* spp. - *Galium*. *Trioxys spinosus*: Europe; *Semiaphis*. Origin: The phylogenetic origin of this complex, because of the parasite group phylogeny, is in deciduous forest type habitats, the present differentiation being, however, very obvious. Relations: It is a typical complex, connected with the steppe type of habitats. It has certain relations with its derivative—Central Asian deserts. The present position of this complex is isolated.

- *North America Steppes (prairies)*. Characteristics: It is typical of steppe type areas of Nearctic America. Distribution: Widely distributed in the Nearctic America, penetrating into various landscapes, due to cultivation namely. No further research has been made (see above). Typical species: *Acanthocaudus caudacanthus*: Wis., Fla.; *Dactynotus* spp. *Acanthocaudus schlingerii*: Brit. Columbia, Calif.; *Dactynotus* spp. *Acanthocaudus tissoti*: Fla.; *Dactynotus* spp. *Aphidius avenaphis*: Ont., to S.C. west to Ind., Calif.; *Myzus*, *Sitobium*, *Rhopalosiphum*. *Aphidius confusus*: Calif., Ariz.; *Dactynotus* spp. *Aphidius floridacensis*: Fla., Tex.; *Dactynotus* spp. *Aphidius nigripes*: Ohio, N.J., Del., Maine, N.C., Mich., Kans., Minn., Calif., Brit. Columbia. *Aphidius obscuripes*: Ont., to N.C. west to Iowa, Colo., Oreg.; *Sitobium*, *Acyrtosiphon*, *Rhopalosiphum*. *Aphidius ohioensis*: Ohio, Tenn., Ark., Ariz., Maine, N.B., Calif., Kans.; *Macrosiphum*, *Dactynotus*. *Aphidius pisivorus*: Wash., Oreg., Idaho, Utah, Nev., Ohio, D.C., Va.; *Acyrtosiphon*. *Aphidius polygonaphis*: Que. to Fla. and Da., west to Wis., and Kans., Utah, N.B., *Dactynotus* spp. *Ephedrus californicus*: Utah, Idaho, Oreg., Ariz., Calif., B.C.; *Acyrtosiphon*, *Macrosiphum*, *Rhopalosiphum*, *Dactynotus*. *Ephedrus incompletus*: N.B. to Fla., west to Kans.; *Macrosiphum*, *Dactynotus*, *Microperus*. *Lysaphidus adelocarius*: Utah, Idaho, N.B.; *Capitophorus*, *Pseudepanerhaphis*. *Lysaphidus ramiithyrus*: Utah; *Capitophorus* spp. *Lysaphidus rosaphidis*: N.J., N.C., Ohio; *Capitophorus* spp. *Lysiphlebus flavidus*: Ohio, Nebr., Colo.; *Aphis* spp. *Lysiphlebus fuscicornis*: Ont., Conn., Tenn., S. Dak., Idaho, Calif.; *Aphis* spp. *Lysiphlebus kuowltoni*: Utah, Idaho, Oregon; *Aphis*, *Microsiphum*, *Myzus*. *Lysiphlebus testaceipes*: All U.S., Mexico, West Indies, S. America, Hawaii (introd.), *Aphis*, *Myzus*, *Toxoptera*, *Schizaphis*, *Macrosiphum*, *Sitobium*, etc. *Monoctonus paulensis*: Alaska, Oreg., Calif.; *Acyrtosiphon*. *Praon aguti*: Ont. to Va., and Ohio, Mass. *Macrosiphum*, *Acyrtosiphon*. *Praon artemisaphis*: Utah, Wash., *Macrosiphum*. *Praon occidentalis*: Ont., Nev., Oreg., Calif., Idaho; *Acyrtosiphon*, *Macrosiphum*. *Praon simulans*: S. Canada and north U.S., Maine; *Acyrtosiphon*, *Macrosiphum*. *Praon unicus*: Wash., Colo. Calif.; *Macrosiphum*, *Phorodon*, *Dactynotus*. *Praon virginianensis*: Va., Ohio, N.Y.;



Fig. 281. Faunistic complexes of parasites - Malaysian. ■ *Archaphidius greenideae*, ▤ *Lipolexis oregmae*, ▥ *Lipolexis scutellaris*, ● *Bioxys japonicus*, ▧ *Paresia tropicalis*, ⊙ *Trioxys confucius*, ⊖ *Tr. sinensis*, ⊕ *Tr. struma*.

Macrosiphum. *Trioxys bonnevillensis*: Idaho, Utah; *Capitophorus*, *Pseudopaneibaphis* *Trioxys corsicanus*: Colo., Utah, Idaho; *Macrosiphum* spp. Origin: The principles of origin will be probably similar as in the Eurasian Steppes type complex, although the Nearctic steppes are much older than those of Eurasia. Some ecological vicariants may occur. Relations: It does not seem to have certain relations to other complexes, except, may be, the presumed Nearctic Deserts complex.

- *Central Asian Deserts* (Fig. 280). Characteristics: Typical of the semi-desert areas of C. Asia. Distribution: Distributed mainly in semi-desert and desert areas of C. Asia, penetrating either to Asia Minor or to the Far East. Typical species: *Lysiphlebus desertorum*: C. Asia, *Cryptosiphum*-*Artemisia*. *Trioxys asiaticus*: C. Asia, Asia M., Far East; *Acyrtosiphon gossypii*. Note: Further research of this complex is necessary, it is believed to be more numerous. Origin: It is probably a derivate of the steppe fauna. Relations: Taxonomic criteria show the relationship to the Eurasian Steppes complex.

- *Malaysian*. (Fig. 281) Characteristics: It is typical of the tropical forest of Malaysia (at least of the Far Eastern districts). Distribution: It is distributed widely in the Far East, in the tropical rain forest districts, its wider distribution is but poorly known. Typical species: *Archaphidius greenideae*: Far East (Taiwan), *greenideae* spp. - *Ficus*. *Lipolexis oregmae*: Philippines, *Oregma lanigera*. *Lipolexis scutellaris*: Far East (S. China, Taiwan); *Aphis* spp. - *Citrus*. *Bioxys japonicus*: Far East; *Callipteris* aphids-*Ficus*. *Trioxys confucius*: Far East, (S. China, Taiwan), *greenideae* spp. - *Ficus*. *Trioxys sinensis*: Far East (S. China, W. Pakistan); *Toxoptera* sp. - *Citrus*. *Trioxys struma*: Far East (Taiwan); *Megoura citricola*-*Ficus*. Origin: It seems to represent a derivate of the Tertiary deciduous forest. The separation is either of Tertiary or Quaternary age. Relations: It has certain affinities to the Far Eastern Deciduous Forest complex. Otherwise at least a part of it seems to be an isolated group, being parasites of Green-

ideid aphids. Note: This complex includes apparently several complexes, which will be distinguished after more material is available.

– *Neotropical*. Characteristics: The complex may be classified for the time being as typical of certain parts of the neotropical America. Its further relations, taxonomic affinities, etc. are still unknown. Typical species: *Lysaphidus plateusis*; Argentina, Tucumán, etc.; *Toxoptera*, *Aphis*, *Rhopalosiphum*, *Brevicoryne* etc. Note: This is also a preliminary classification.

– *Subantarctic Forest*. Characteristics: For the time being this complex is indicated by the occurrence of its probable elements—parasites of certain primitive Callipterine aphids—*Pseudephedrus neotropicalis*, in Cuban Tropical Cloud forest. This complex is believed to occur mainly in the mountainous parts of the south of Neotropical America, its elements penetrating to the north (mountain zone). Typical species: *Pseudephedrus neotropicalis*: Cuba (and probably all the mount. parts of S. America); *Neolizerius* spp.

– *INFLUENCE OF GEOLOGICAL PERIODS*. Owing to close connection of the parasite distribution with different floras and aphid fauna, it is clear the influence of geological periods on the fauna of parasites has a similar influence, although the results are specific for the parasite group itself.

Judging from the fossils, recent distribution and host specificity of the Aphidiidae, it seems that in the Tertiary the most numerous and common were the aphid parasites occurring in coniferous and deciduous forest types.

The Quaternary has deeply influenced also the parasite fauna. The separation of the primarily more or less continuous zonal belts of floras caused the separation of the parasite faunas, the separate parts being under different influences of climate, etc. During this period, the original faunas of coniferous and deciduous forests were partly suppressed, partly retreated to refugia, following the floras. The end of the Tertiary and the Quaternary (interglacial) also influenced and caused the origin of steppes and the corresponding adaptation of floras and faunas to the new environment.

The contemporary state of research of the aphidiid fauna allows us to suggest the following about the recent parasite fauna in accordance with the influence of geological periods:

1. Coniferous and deciduous forest faunas were suppressed in the Quaternary.
2. Deciduous forest fauna gave origin to the steppe fauna.
3. Steppe fauna is younger, representing the most progressive direction of parasite development. This is rather important for biological control of agriculture pests.
4. Certain parasite groups adapted to cooler conditions and invaded the forest-tundra zone and related zones.
5. The coniferous and deciduous forest faunas have been also in a period of convalescence and further progress.

– *THE CONTINENTS*. Although the separate faunistic complexes are basically zonal in distribution, it is useful for biological control purposes to list the established complexes in separate continents:

Eurasia: Holarctic Forest Tundra, European Boreal, West Eurasian Coniferous Forest, East Eurasian Coniferous Forest, European Deciduous Forest, Far Eastern Deciduous Forest, Eurasian Steppes, Mediterranean, Central Asian Deserts, Malaysian, introduced spp. (accidentally, biol. control).

Africa: Mediterranean (elements), European Deciduous Forest (elements), further presumed faunistic complexes, introduced spp. (accidentally).

Australia: Parasite fauna almost unknown. Introduced spp. (accidentally, biol. control).

North America: Holarctic Forest Tundra, North American Coniferous Forest,

North American Deciduous Forest, North American Steppes (prairies), presumed complexes, introduced species (accidentally, biol. control).

South America: Neotropical, Subantarctic Forest, North American Steppes (elements), presumed complexes, introduced species (accidentally).

Antarctica: Parasite fauna unknown.

— MUTUAL CONNECTIONS. The mutual connections among the separate ancient complexes in the past may be recognized when evaluating the influence of the three main factors: (1) The zones of floras were primarily more or less continuous, (2) Separation of continents, (3) Influence of the Quaternary. When this historical aspect, the details of which have been dealt with above, is used, the connections of the derived types with their original complexes are distinct.

Deciduous Forest of the Tertiary: Far Eastern Deciduous Forest, European Deciduous Forest, North American Deciduous Forest.

Coniferous Forest of Tertiary type: East Eurasian, West Eurasian, North American Coniferous Forests.

Further differentiation developed in the separate regions mostly independently, the original connection remaining clear. The steppe fauna developed probably independently. A peculiar position has the Quaternary circumpolar forest tundra complex. It is a very young complex, and due to the homogeneity of circumpolar floras it spread almost all over these habitats, although it seems to be Palearctic (European) in origin.

The two main ancient original complexes, coniferous and deciduous forests, have a great influence on the relations among different faunistic complexes of today.

Principally, both coniferous and deciduous forest types represent, as to their aphid and parasite fauna, strongly different and isolated types. Also in case of a mixed forest, the fauna is strictly dependent on either coniferous or deciduous trees. Nevertheless, there are certain though few mutual relations, all being clearly of secondary character.

The coniferous forest complex has the following elements spread in the deciduous forest:

Panisia maculolachni: The lachnid host aphid (*Maculolachnus submacula*) occurs on Rosa and it is a lachnid species secondarily adapted to deciduous shrubs. Similarly, the parasite is a member of the genus that occurs almost exclusively in coniferous forest habitats.

Other cases of this type might be mentioned, from other areas, too—*Panisia tropicalis* in the Far East, etc.

Protaphidius spp.: The parasites are clearly related to the parasites of Quaternary aphids occurring in coniferous forests (*Panisia*). Because of the secondary adaptations of the *Stomaphys*-aphids to deciduous forest conditions, the parasites occur in the deciduous forest, too.

On the contrary, a deciduous forest complex has the following elements spread into the coniferous forest:

Praon bicolor: It is a member of the genus that is connected with the Lachnidae only exceptionally, occurring mostly in deciduous forest and steppe to semi-desert habitats. The parasite mentioned is the only species occurring in a coniferous forest, being a parasite of the lachnid *Protolachnus*, which is a typical coniferous forest aphid species.

Lysaphidius schimitscheki: It is a parasite of *Liosomaphys (Elatobium) abietina*. The aphid is clearly an element of a deciduous forest that adapted secondarily to coniferous trees and coniferous forest habitats. The other species of the parasite genus are connected mostly with aphids that live in steppe type habitats.

Nevertheless, also in the case of penetration of coniferous trees to the steppe type habitats, the fauna of aphid parasites has no relations to the neighbouring (steppe)

habitats. This is, no doubt, due to the strict specialization of the aphids to coniferous trees, and of the parasites to these aphids. Similarly, because of the zonation of forests, coniferous forests (taiga) have usually no direct connections or transitional zone with the steppe zone, like "coniferous forest-steppe zone".

The deciduous forest, on the contrary, has rather strong connections with the steppe. Transitional zone—forest-steppe—occurs. A number of deciduous forest elements penetrated into not only the transitional zone, but occur in various places of the steppe landscape.

This has a corresponding influence on the fauna of parasites. A number of dioecious aphids occur on the edges of forests on primary host plants and migrate from there to the secondary host plants in the steppe. In this way, they come directly into contact with the deciduous forest fauna. Because of such features, we might subdivide the deciduous forest parasite fauna into deciduous forest fauna s. str. which is typical of the deciduous forest and its true habitats, infesting the typical deciduous forest aphids, too; furthermore, the parasites that occur mostly in the deciduous forest transitional zone are typical of the edges of deciduous forests, forest steppe, etc. The latter group may penetrate to a certain degree to the steppe. All this is also conditioned by zonation, temperature and humidity conditions.

Similar relations and connections exist between the steppe and semi-desert, or desert fauna.

—*Eurasia and North America.* During long geological periods the two continents were separated by the sea and separate faunas developed. Some connections which were not few, the last of them covering the district of the Bering Sea, occurred. The last one mentioned was very young from the geological viewpoint—in the late post-glacial periods—and exchange of faunas followed. We may summarize the relations of Palearctic and Nearctic regions that because of the formation of faunas of different sources, the distinctness is primary and the similarity is secondary. Both Eurasia and N. America are connected with various regions, the elements of which often penetrated far to their border areas. The principal landscapes are rather heterogeneous. The original zonation is similar, but the belts were later modified due to the influence of geological periods. Today's centers of deciduous forests—W. Europe, Far East and south-eastern parts of the Nearctic—are widely separated today, Eurasian steppes are entirely separated from the N. American steppes and deserts. Besides, the mountain ranges have a different direction, introducing the elements of inter-zonation to the original belt zonation.

In accordance with our studies on the aphidid parasites, we may stress LINDROTH's (1957) conclusions: "With land forms the proportion of identical species falls rapidly with decreasing latitude, where the width of the Atlantic Seas is greater and where the important Bering Strait land bridge becomes less effective". If we summarize the connections between different belts of Palearctic and Nearctic and corresponding faunistic complexes, the following results may be obtained:

Holarctic Forest Tundra complex is identical. It is the only complex that shows the distinct connection between the Palearctic and Nearctic aphidid fauna. Because of its exclusive position in this complex, it will be dealt with here in more detail: The zoogeographic position of the two main members of this complex is evaluated to show the development of relations between the Palearctic and Nearctic Forest-Tundra complexes. *Aphidius cingulatus* is strictly specialized to the Pterocommatine aphids. Because of this close specificity we may derive some conclusions from this relation: The Pterocommatine aphids are mainly associated with willows (*Salix*), to a lesser degree with poplars (*Populus*), this being of secondary character. They are distributed in the Holarctic, although the distribution of their host plants is much

wider. From the 6 genera known 2 occur in the western parts of the Palearctic region, 2 in the Nearctic and 2 are common for both the regions. Three centers of origin of the Pterocommatinae, the Nearctic, the West Palearctic, and East Palearctic, may be recognized. The Nearctic and West Palearctic show a great relationship—vicariants often occur, being an indicator of their original homogeneity. If the development of various groups of willows is taken into consideration (SZELEGIEWICZ, 1965), it seems that this aphid group evolved in the western part of their Eocene distribution area. This area was at that time occupied by Arcto-tertiary flora (Alaska, Canada, Greenland, N. Europe, over 57° north lat.). Owing to the climate becoming cooler, they retreated to the south, and after the disappearance of the land bridge between N. America and Europe they evolved in vicarious forms and genera. As to their distribution in East Asia, they reached it either earlier from N. America, or later from Europe (geogr. races). In the Quaternary, the extremely variable Pleistocene climate stimulated a new wave of evolutionary processes among the willows. While no trace of parallel evolution of the Pterocommatinae with Salicaceae may be recognized in the Tertiary, a certain convergence may be noted in the Quaternary because of the appearance and development of certain aphids, too. When evaluating the recent distribution of the Pterocommatinae it is obvious that they are connected to temperate and we may say to cool parts, of the Holarctics. This corresponds, in our opinion, to the general trend of their evolution. Many species might be characterized as just examples of the forest-tundra (N. Europe, Iceland, Greenland, etc.). In spite of their recent distribution, the Palearctic and Nearctic species are mostly different. As mentioned above, *A. cingulatus* is a strictly specialized parasite of the Pterocommatinae. Because of its distribution, it is obvious that it was originally a European element, which spread after the Quaternary to N. Europe – Iceland – Greenland to N. America, where it is widely distributed today. Similarly as its hosts, it is distributed to Kazakhstan in the Palearctic region, but being unknown in the Far East, although the aphidid fauna of this district is comparatively well known. This shows that the origin of the parasite was probably somewhere in the western parts of Eurasia.

Lysiphlebus salicaphis. This is a parasite of *Chaitophorus* spp. and allied genera. In our opinion the Chaitophorid aphids may be also classified as an aphid group well adapted to the cool climate, their spread to the forest tundra habitats being typical. The route of spread—Europe – Iceland – Greenland – N. America—is the same as in the previously mentioned species. But it is known from the Far East (probably via C. Asia, or circumpolar in distribution).

Aphidius salignae seems to be a somewhat different case, being still not yet clear. It is a parasite of *Tuberolachnus salignus*, a Lachnid aphid, associated with willows. As the parasite has been described from the Far East, it might be a member of the Deciduous forest complex, although it has been found in California as well (STARÝ & SCHLINGER, 1967); the route via the Far East – Bering strait – Pacific coast might be possible; further records are necessary.

European Boreal faunistic complex is connected with the similar habitats to the forest-tundra species. Its distribution in Europe shows its post-glacial character. It may be classified as a complex of species that is post-glacial in origin, but apparently has not been able to spread as the Holarctic Forest Tundra complex has to N. America via Iceland. The main group of this complex are members of the genus *Diacretellus*, being mostly connected with peat bogs.

Taiga: the species have no apparent relations except for the main generic composition. The same may be said of the steppe and desert faunas.

European Deciduous Forest faunistic complex has no connections with the Nearctics. Few species have penetrated as far as Iceland, following the forest-tundra

communities, in which they also occur in Europe (*Ephedrus plagiator*, *Praon volucre*).

The following species were introduced from Eurasia into N. America. They are today often common members of Nearctic communities, being, however, of west Eurasian origin and their introduction is quite recent: A. Accidentally introduced: *Aphidius hortensis*, *A. matricariae*, *A. ribis*, *A. rosae*, *Ephedrus persicae*. B. Biological control introductions: *Praon exoletum*, *Trioxys complanatus*, *Tr. pallidus*, *Aphidius matricariae* and others (see: Biological control).

– *Europe and Far East*. This relation has been dealt with above in some detail and only the main connections are mentioned here. The Far East fauna deeply influenced both the coniferous and deciduous forest fauna of Europe, being the original fauna from which the European complexes are derived. On the contrary, elements of the Eurasian steppes and C. Asian deserts are primary, penetrating into the Far East.

– *Europe, Far East, Nearctic America*. A comparative list of the genera of the Aphidiidae shows the principal features of the fauna of these regions. We may conclude that the Far Eastern fauna is the most ancient and no doubt original, having the influence and connections with the European fauna and other Eurasian fauna. The Nearctic America mostly shows only very ancient affinities to the Eurasian fauna. On the other hand, the affinities may be found to be very young, being common in the circumpolar forest-tundra zone.

– *PARASITES*. The main trend of evolution of aphids and their aphidiid parasites was identical, as has been mentioned in the phylogeny chapter. Both groups, however, have their own phylogenetical features. There is no doubt of the faunistic complexes existence in the aphid fauna, which will have certain typical features, similar to those of the parasite complexes (zonal distribution, connections with separate floras, etc.). Because of the host – parasite relationship development (see: Host specificity) the old groups of hosts may be attacked either by old species of parasites, or by the young and widely specialized species. This is true both with regard to aphids and their parasites, where host – parasite phylogenetic parallelism may be found in a comparatively low number of cases only. Thus, although faunistic complexes may be recognized both in the fauna of hosts and parasites, they possess certain specific features in accordance with the development of both the groups; the host – parasite phylogenetical parallelism rule cannot be generally applied here although it may be true for some cases of specialized parasites.

– *CULTIVATED LANDSCAPE*. The relation of the cultivated landscape and the faunistic complexes of parasites is of basic significance for the biological control of aphids.

According to our studies, the cultivated landscapes include on the one hand typical cultivated elements (crops), on the other hand, there are always included some remains of the original landscape or communities which are deeply influenced by cultivation. Apparently, the parasites adapted themselves to a certain degree to the partly cultivated landscape as many species may be found today commonly occurring in crop growing areas.

In European orchards, which have many features of forest-type habitats, there occur species of the European Deciduous Forest faunistic complex. Similarly, the field crops are often inhabited by the Eurasian Steppes faunistic complex, which covers also the waste places, ruderals, and similar places that developed due to the cultivation.

Similar parasite complexes and cultivated lands dependence have been observed in other visited countries too (C. Asia, Caucasus, Cuba), so that the feature mentioned seems to be true in a general way. Therefore, the cultivated landscape cannot be separated, moreover, it has many close connections with the original uncultivated areas, the faunistic complexes of parasites responding in a similar way.

It is necessary to stress, in addition, that the cultivated steppe may be classified as a

kind of steppe type district. As has been mentioned, the steppe zone is just the zone of most extensive aphid and parasite development. The growing of various crops, monocultures, has created simultaneously favourable conditions for the occurrence of various pest aphids and their parasites.

— GREENHOUSES. The aphids occurring in greenhouses in the temperate zone are of two groups: The first group includes aphid species of tropical and subtropical origin, which have been distributed in the greenhouses by man's activity when transferring or introducing plants, nevertheless, they are restricted to the heated greenhouse conditions: they are unable to overwinter in the open occurring there possibly only during the summer period. The second group of aphids covers the indigenous aphids that invaded the greenhouse either accidentally or were introduced there with plants: they may or may not overwinter in the greenhouse.

We know no records, either literary or of our own, that tropical aphidid parasites would also be introduced in temperate zone greenhouses; the parasite fauna of greenhouses, therefore, consists of the indigenous parasites of the neighbourhood of the greenhouse, the species penetrating into the greenhouse and parasitizing the aphids living inside, if the latter were found suitable although they are tropical in origin. The indigenous aphid species occurring in a greenhouse were found and probably are generally parasitized by the indigenous parasites in the same way as in the open in case a parasite species invades the greenhouse. There is only one case known, that of *Aphidius matricariae*-strain in California, where the parasite strain had apparently been introduced into California greenhouses, but it failed to establish in the open (see SCHLINGER & MACKAUER, 1963).

— THEORY AND PRACTICE. The division of the aphidid parasite fauna has been based on several years' research of the taxonomy of the group as well as on ecological studies. On such a basis, literature records being used as well, the comparison of the fauna of separate continents was made with respect to hosts and host specificity influencing factors. As a result, we have found that one aphid species is often attacked by different parasite species in various parts of the world. The research of such sources has shown that there are apparently several centers of origin recognizable in the world fauna of parasites. As we had a good knowledge of European fauna, the results of some of our research trips to other countries being at hand as well, we started further research work on the geographical distribution of separate species with respect to the ascertained habitat dependence and other host specificity influencing factors. We have ascertained that the parasites are attached to certain floristic zones, and then it was easy to apply this feature on the development of floras, resulting in the understanding of basic records on parasite distribution—the main faunistic complexes of parasites have been established.

Therefore, the natural conditions seem to be the best proof of our theory, showing the difference in parasite composition of the same or closely related hosts in various parts of their distribution area.

The research of Californian authors when searching for various parasites in a subtropical belt, in the zones allied to Californian conditions, seems to be simultaneously an incidental proof of our research results as well, as the climatic belts mostly represent areas of certain peculiar floras, i.e. the search for parasites in the same climatic zone means also that the parasites may be restricted in distribution in dependence on the climate. As the climatic belt was found to exhibit certain features, there was apparently another reason—although climatically apparently dependent—that the parasites were different in different parts of the given subtropic belt. From this viewpoint, too, the dependence of parasites on floristic zones has been ascertained, or better to say, proved as well.

Island Fauna

Islands are commonly separated into two groups: The first group includes the continental islands, which represent really detached fragments of a mainland. They possess a much larger number of species than the oceanic islands, the number of genera too being larger. The second group—the oceanic islands—are the true free islands, which have had no previous connection with the mainland, from which the flora and fauna now existing on them could be derived.

The separation of islands has been commonly used, although it is relative, being true to a various degree in separate cases. Strictly said, the fauna of islands that had been separated from the mainland not long before, as well as fauna of young oceanic islands, corresponds really to the above mentioned classification (for example, the British Isles – Krakatau).

In our opinion, such a classification is no doubt relative, as a different period of time has been connected with the isolation of separate islands. Nevertheless, although being relative, such a classification is highly important for the general classification of the given island fauna to understand its development and origin.

Floristic criteria seem to be rather helpful. As we now know approximately all the methods of seed-dispersal, we are in a position definitely to state that the occurrence of certain types of plants in any island is strong evidence that the island must have been formerly attached to a mainland (RIDLEY, 1959).

A REVIEW OF CERTAIN FAUNAS. For separate faunistic complexes distribution see figs. 273–281.

– A. CONTINENTAL ISLANDS. Of these we may deal here more extensively with the following:

– *British Isles*. The British Isles exhibit—in connection with their geological history—typical features of the European fauna. There are apparently present almost all the species that occur in the neighbouring parts of Europe. Otherwise, all the faunistic complexes occurring in Europe have been established in the British Isles as well with the exception of the Mediterranean faunistic complex, but it is possible that *Monoclonia pistaciaecola*, following *Pemphigus* aphid hosts has reached the Islands, too.

Holarctic Forest Tundra faunistic complex. (*Aphidius emgulatus*, *Ephedrus brevis*, *Trioxys betulae*, *Tr. compressicornis*, *Lysiphlebus salicaphis*, *Trioxys ibis*, etc.). From the zoogeographical point of view this complex is the most important showing the migration route Br. Isles – Iceland – N. America.

Boreal Europe faunistic complex. (*Diaretellus ephippium*, etc.).

West Eurasian Coniferous Forest faunistic complex. (*Panesia picta*, etc.).

East Eurasian Coniferous Forest faunistic complex (*Panesia abietis*, *P. infusata*, *P. laricis*, *P. pinii*, *P. nililachni*).

European Deciduous Forest faunistic complex. (*Aphidius hieraciorum*, *A. hortensis*, *A. lonicerae*, *A. ribis*, *A. rosae*, *Arcopraon lepellei*, *Dyscritulus planiceps*, *Ephedrus minor*, *Lysiphlebus ambiguus*, *L. dissolutus*, *Monoclonus caricis*, *M. cerasi*, *M. crepidis*, *M. nervosus*, *M. pseudoplatani*, *Praon abjectum*, *P. flavinode*, *P. volucre*, *Toxares deltiger*, *Trioxys angelicae*, *T. heraclei*, *T. letifer*, *T. cirsti*, *T. pallidus*).

Far Eastern Deciduous Forest. (*Aphidius salicis*, *Ephedrus lacertosus*, *E. persicae*, *E. plagiator*, *E. validus*).

Eurasian Steppes faunistic complex. (*Aphidius absinthii*, *A. avenae*, *A. crvi*, *A. funebris*, *A. matricariae*, *A. pastorum*, *A. souchi*, *Lysiphlebus fabarum*, *Paralipsis cucumis*, *Praon absinthii*, *P. dorsale*, *P. exoletum*, *Trioxys aculeatae*, *T. brevicornis*, *T. centanrae*).

– *Iceland*. The parasite fauna of Iceland is almost fully characterized by the presence

of members of the Holarctic Forest-Tundra faunistic complex, *Aphidius cingulatus* and *Trioxys compressicornis* being established and the other members of this complex—being known both from the northern parts of Europe and N. America—are expected to be found in the future as well (*Trioxys betulae*, *T. ibis*, *Lysiphlebus salicaphis*, *Ephedrus brevis*, *Aphidius sicarius*).

Two members of the European Deciduous Forest faunistic complex have been established too (*Praon volucre*, *Ephedrus plagiator*). Both are widely distributed and widely specialized species, occurring from northern to southern areas of the corresponding communities. Their occurrence in Iceland is in apparent connection with their ability to penetrate to north forest tundra communities, where they may still find some host aphids. Both species have been established in the British Isles, nevertheless, none of them seems to be able to spread farther to the Nearctic America, this corresponding fully to their ecological characteristics. The faunistic position of *Monoctonus caricus*, which may commonly be found in grassland habitats in the island, is not yet clear.

— *Greenland*. Although a peculiar fauna of aphids has been found to occur in Greenland, only *Aphidius cingulatus*—a member of the Holarctic Forest Tundra faunistic complex—has been established there as yet. This is in close connection with the migration route of other elements of this complex, southern parts of Greenland being apparently covered as well when the species reached the N. American area of forest-tundra zone.

— *Cuba*. Its geological history has been marked by up and down oscillation. Land connections have occurred in the past with S. America, C. America and the Floridan area of N. America, as well as connections between the separate islands in the West Indies which have also been continuous during certain periods. The flora belongs to the Neointertropical region. Cuba does not possess an original fauna of aphid parasites. This may be understood both from the geological history and spreading possibilities of aphids and parasites. Although there are some species which have been known to occur in Cuba exclusively, this is due to the poor knowledge of the group in the neighbouring continents and all such species are believed to have been later ascertained in at least some of these countries.

The comparatively low number of parasite species occurring in Cuba allows us to classify the fauna very clearly, the following groups of species being recognized:

Cosmopolitan species. *Diactetiella rapae* is a typical representative of this group, although it seems originally to have been a member of the Eurasian Steppes faunistic complex.

North American Steppes faunistic complex. This complex has the most important influence on the fauna of the parasites of Cuba. Species of this complex are predominant in the Cuban fauna of parasites. Some of them have been known from the south of the U.S.A. (Florida), the others are more widely distributed in the Nearctic region. The following species may be mentioned as the representatives: *Ephedrus incompletus*, *Aphidius floridaensis*, *Lysiphlebus testaceipes*, *Acanthocaudus tissoti*.

North American Coniferous Forest faunistic complex. Some members, which are connected with the coniferous forest zone, penetrate southward, *Pauesia* sp. (mummies only) was found as a parasite of *Quercus* spp. in Cuban pine forests. Because of the occurrence of members of this complex in Florida, this may be easily understood.

Subantarctic Forest Faunistic complex. Although this complex is not satisfactorily known, it is presumed to be connected with the south of the Neotropical region, penetrating far to the north—following the mountain ranges and tropical cloud forest community. *Pseudephedrus neotropicalis* is a typical representative of this complex, being a parasite of a primitive Callaphidid aphid (*Neolizerius* sp.).

The Cuban aphid parasite fauna has therefore the closest connection with the steppe zone of N. America, to a lesser degree with the coniferous forest zone of this region. Cosmopolitan species are also less numerous. Elements of the neotropical fauna can be found in the tropical cloud forest zone, being uncommon.

—*Japan*. The Japanese islands represent a similar case as the British Isles in Europe, except that they are on the eastern shore of the Eurasian continent, being about 16° further south and having a greater extension in latitude.

In a corresponding way, there are various faunistic complexes of parasites represented in the Japanese islands. The separate islands (Kyushu, Honshu and Hokkaido) seem to exhibit certain differences among themselves as to the occurrence of some species, which is natural due to the different latitude and corresponding different floristic features.

Generally, the Japanese islands resemble the neighbouring continental areas, which possess similar features as may be recognized from the comparison of the parasite fauna of Taiwan, Hong Kong, South Korea and Japan (STARÝ & SCHLINGER, 1967).

As to the endemism of species mentioned in the book of STARÝ & SCHLINGER (1967) the same may be said as in the case of Taiwan. According to our present opinion (STARÝ, 1967), there are no endemics of a given area, but there are species connected with a certain floristic zone. Therefore, if any species are known to occur in the Japanese islands exclusively, they cannot be classified as being endemic as they will apparently be ascertained to occur in other areas where the given floristic zone is distributed.

The following faunistic complexes of parasites are represented in the fauna of the Japanese islands:

Holarctic Tundra faunistic complex. The occurrence of its members is probably due to the occurrence of *Lysiphlebus salicaphis* in S. Korea.

East Eurasian Coniferous Forest faunistic complex. *Diaretus leucopterus*, *Pauesia infusata*, *P. laricis*, *P. inouyei*, *P. jezoensis*, *P. konoi*.

Far Eastern Deciduous Forest faunistic complex. *Protaphidius uawaii*, *Lysiphlebia japonica*, *Ephedrus persicae*, *E. plagiator*, *Pauesia japonica*, *Trioxys brunneus*, *Aphidius areolatus*, *Praon orientale*, *Monoctonus similis*, *Aphidius gifuensis*, *A. salignae*, *Praon glabrum*, *Aphidius salicis*.

Eurasian Steppes faunistic complex. *Diaretiella rapae*. The species, besides the mentioned cosmopolitan one, seem to be more widely distributed in Japan.

Malaysian. *Bioxys japonicus*. Although the separate members of this complex seem to be distributed in connection with the floristic zones—in the true oriental region areas—they will be apparently found in some southern areas of Japan as well.

—*Taiwan*. According to our book (STARÝ & SCHLINGER, 1967), this island has the largest recorded aphidiid fauna in Far East Asia, containing 21 species in 12 genera and subgenera. According to the earlier opinion of the authors, some of the species and genera were mentioned as endemics of this Island. Our recent opinion differs from our earlier point of view. The careful examination and comparison of the fauna of the district of Taiwan, Hongkong, S. Korea and Japan has shown, in accordance with our general studies on the geographic distribution of the aphidiids, that the separate aphidiid species do not represent apparently endemic species of certain continental areas or island faunas, but they are members of various faunistic complexes which are also associated with separate floristic zones. The occurrence of certain genera and species being known from a single place corresponds to the inadequate level of faunistic research of the Far East Asian area; such species are expected to be also found later in other districts of the corresponding floristic zones in the Far East Asian area. For example, the genus *Archaphidius* with its single known species

(*A. greenideae*) has been described from Taiwan being also mentioned as an endemic. Nevertheless, we have classified this species as a member of the Malaysian faunistic complex, which is typical of the tropical rain forest of south east Asia, covering mostly parasites of the Greenideid aphids. The probably wider distribution of the genus may be derived from the distribution of the other members of the complex presented.

The following faunistic complexes of parasites have been known from Taiwan:

East Eurasian Coniferous Forest faunistic complex. *Panesia unilachni*.

Far Eastern Deciduous Forest faunistic complex. *Lysiphlebia japonica*, *Monoctonus woodwardiae*, *Ephedrus lacertosus*, *E. orientalis*, *E. persicae*, *Trioxys carinatus*, *Aphidius gifuensis*, *A. salicis*, *A. salignae*, *Praon orientale*.

Eurasian Steppes faunistic complex. *Aphidius absinthii*, *Lipolexis gracilis*, *Diaeretiella rapae*.

Malaysian faunistic complex. *Archaphidius greenideae*, *Trioxys struma*, *Trioxys confusus*, *Lipolexis scutellaris*.

This review clearly shows the various influences of faunistic complexes of parasites that are in close connection with the occurrence of the given floristic zones in Taiwan. — *Philippines*. This island group is unsatisfactorily known until now. Only *Lipolexis oreghanae*, a member of the Malaysian faunistic complex has as yet been ascertained in this area.

— *New Zealand*. This very important and interesting area—both from a basic and applied point of view—has been until now unsatisfactorily studied; *Diaeretiella rapae*, a cosmopolitan species, is mentioned in the literature. Detailed research of the New Zealand parasite fauna would be rather interesting from the zoogeographical point of view, including at least some cases of the southern hemisphere temperate parasite fauna elements.

— *Sicily*. Sicily has a fauna identical with the southern parts of Italy, which is apparently caused by its position. The number of species ascertained in Sicily in 1963 (STARÝ, 1966) is distinctly less compared with the fauna of Italy. We have ascertained 49 species as occurring in Italy, which number nevertheless is much higher in reality, while only 22, less than one half, have been found in Sicily. After careful comparison of the faunistic complexes, hosts etc., this state is believed to be caused by the following factors:

1. Certain floristic zones are almost lacking in Sicily, while they occur in the northern parts of Italy. For example, the true coniferous forest of northern parts of Italy, where a number of *Panesia*-species may be found; the deciduous forest occurs as poor remains in the mountains.

2. The faunistic research has not been detailed enough, as for example some common and widely distributed species of parasites have been found in Sicily while they are unknown in all Italy, although there is no doubt about their occurrence in this area as well.

3. Sicily is characterized by a typically Mediterranean landscape, with prevailing steppe to semidesert zones, besides cultivated areas (orchards, gardens, etc.). the forest zone is relatively scarce and distributed in the mountains exclusively, while a typical Mediterranean shrub-forest association may be seen in some parts of the lowlands, rocky sea-shore, etc.

Therefore, the low number of species ascertained in Sicily is apparently due not to island features but corresponds to the floristic zones.

The following faunistic complexes of parasites have been ascertained in Sicily:

Eurasian Steppes faunistic complex. Its members represent the most typical component of the parasite fauna of Sicily. *Ephedrus campestris*, *Praon dorsale*, *P. exoletum*.

Aphidius avenae, *A. ervi*, *A. pascuorum*, *A. fuscicornis*, *A. sonchi*, *Lysiphlebus arvicola*, *L. fabarum*, *Trioxys centaureae*, *Lipolexis gracilis*, etc.

Mediterranean faunistic complex. It is also very typical of Sicilian fauna. *Aphidius transcaspicus* and *Monoctonia pistaciaecola*.

European Deciduous Forest faunistic complex. Its members have been found mostly in irrigated orchards, gardens, river valleys, etc., to a lesser degree in the true deciduous forest zone, which is poorly preserved on the Island. *Praon abjectum*, *Aphidius rosae*, *Lysiphlebus ambiguus*, *L. thelaxi*, *Trioxys angelicae*, *T. pallidus*.

Far Eastern Deciduous Forest faunistic complex. *Ephedrus persicae*.

West Eurasian Coniferous Forest faunistic complex. Only *Pauesia silvestris* has been found to occur in Sicily, in secondarily afforested sea coast districts (Pinus); nevertheless, some other members of this complex may be found to follow various Mediterranean Pinus associations.

— *Canary Islands*. The Canaries consist of a group of islands, each of which has its own peculiarities. In the western islands there is a subtropic vegetation which becomes poorer to the east, being at last almost absent due to the influence of the west African Sahara Desert. Furthermore, the exposition of the slopes plays an important role in the distribution of plants in each island, and has its role in the vertical distribution of growing different crops as well. The agriculture exhibits distinct subtropical and tropical features (bananas, sugar cane, tomatoes, tobacco, corn, citrus, etc.).

The parasite fauna is poorly known. Only some swept material has been identified by MACKAUER (1962). Judging from this material, the following faunistic complexes occur in the Islands:

Eurasian Steppes faunistic complex. It seems to be (naturally) the most distributed complex, including the species: *Aphidius ervi*, *A. avenae*, *A. matricariae*, *Diaeretiella rapae*, *Trioxys paenonicus*, *T. brevicornis*.

European Deciduous Forest faunistic complex. *Praon volucre*, *Lysiphlebus ambiguus*, *Aphidius rosae*, *Trioxys angelicae*.

Far Eastern Deciduous Forest faunistic complex. *Ephedrus persicae*.

The parasite fauna of the Canaries exhibits typical features of the Mediterranean area, although the number of species found is much lower. Nevertheless, this is apparently due also to the initial stage of investigation; no detailed research has been undertaken as yet, the swept material being apparently collected in the cultivated landscape, the natural communities being omitted.

— *OCEANIC ISLANDS*. These are represented by the following examples.

— *Bermuda Islands*. The aphid fauna fully corresponds to the oceanic character of the islands. The results of the research (MAGGILLIVRAY 1959) have shown that the greatest part of species established represent common species that are widely distributed in the West Indies, southern parts of the U.S.A., etc., while there are no species attached to natural communities of the island as can be seen in the West Indies, which are continental as to their origin. The aphid fauna of the Bermudas may be therefore classified as a previously immigrant aphid fauna from the neighbouring areas. The same situation seems to be true of the parasite, where only one parasite species, *Lysiphlebus testaceipes*, has been ascertained (WATERSTON, 1944), being widely distributed over the Nearctic, and the West Indies as well, penetrating to the tropics of S. America.

— *Hawaii*. This group of islands is 700 miles from the nearest Polynesian islands, and 2350 miles from America. It has a very rich flora, suggesting that it was formerly of a much wider extent, and that it is of great antiquity. Some of the genera contain a considerable number of species which is not at all usual in oceanic islands, and it

includes a number of genera otherwise absent in such islands. There is a distinct American element and it is difficult to see how such plants, with American affinities, could have passed over 200 miles of sea (RIDLEY, 1959).

Because of various influences, the present day fauna of parasites exhibits the presence of members of various origin:

Far Eastern Deciduous Forest faunistic complex is represented by *Aphidius gifuensis*.

North American Steppes faunistic complex. *Aphidius obscuripes*, *Ephedrus incompletus*, *Monoxotomus paulensis* and *Lysiphlebus testaceipes*—introduced (see below).

Cosmopolitan species. *Dianthella rapae*; being originally a species of Eurasian Steppes faunistic complex, is almost cosmopolitan today, its presence in Hawaii is apparently due to accidental introduction from the U.S.A.

Introduced species. *Lysiphlebus testaceipes*—introduced in 1923 and 1965, originally a member of the North American Steppes faunistic complex. *Aphidius smithi*, originally from India, introduced to Hawaii via California insectaries.

Species of the Nearctic faunistic complexes play the major role as to specific composition, being apparently a result of accidental immigration by man's agency. To a lesser degree, members of the Far East Asian and cosmopolitan species are present, not to mention species introduced purposely.

Note: ZIMMERMANN (1948) has grouped the Hawaiian biota as follows: (1) Native. They are either indigenous (live naturally in Hawaii as well as in some other place or places, and whose distribution came about without the intervention of man), or endemic (entirely restricted to Hawaii). (2) Foreign. They may be either immigrant (unintentionally brought in by the intervention of man), or purposely introduced. According to this classification, which has been used for the Hawaiian insects, all the parasites of aphids belong either to immigrant or purposely introduced species.

—Guam. The aphid fauna of this island has been dealt with by SWITZER (1942). It exhibits typical oceanic island features, being represented by common species—immigrants, such as *Rhopalosiphum maidis*, *Aphis craccivora*, *Aphis gossypii*, *Pentalonia nigroviridis*, etc. No aphidid parasites have been observed, *Aphelinus*-species being the single parasite mentioned.

4. Ecological classification. Aphids in islands as well as in the continents are more or less connected with certain floristic zones or communities. Some species are typical for coniferous forests, others for deciduous forest, steppe, desert, etc., these zones being further subdivided with respect to geological (including climate) history of the separate areas. Therefore, in accordance with the classification of plant communities in an island, we can distinguish the separate groups of aphids in a corresponding way. There are many inter- and trans-zonal elements, they nevertheless do not influence the main features of a scheme carried out.

5. Ecological groups. Similarly as in continental areas, the aphids occurring in islands may be grouped into the freely living aphids, leaf-curling aphids, gall aphids, root aphids, etc. Various types are represented to a various degree, being dependent on climate, presence of certain host plants, etc.

6. New crops. Practically every new crop that is introduced to be grown in a certain island area may be expected to be attacked by aphids. The aphids may originate from the following groups:

(a) "Indigenous", i.e. the aphids that had occurred in the island before the crop was introduced.

(b) Aphids – new immigrants. In this group aphids belong which do not occur in the island, due to lack of host plants, but it is probable that they soon appear—namely if being common in the neighbouring mainland—as far as the new crop is grown.

7. Greenhouses in islands as an aphid environment seem to exhibit the same features—as to the composition of species—as the greenhouses in the continents. As far as we can judge from the comparatively few records available, the number of aphid species is apparently lower in connection with the generally low number of species present in a given island.

– PECULIARITIES OF ISLAND PARASITE FAUNA. Island faunas exhibit various peculiarities, which occur to a various degree in various islands. Generally, the continental islands exhibit less peculiarities, while the oceanic islands are very different.

– *Specific composition.* The comparison of island faunas and the neighbouring continents has shown that, be an island of continental or oceanic type, its fauna consists of a distinctly less number of species than the neighbouring continents. Oceanic island fauna of parasites seems to be extremely poor.

– *Habitat requirements.* In continental islands, the habitat requirements of the species seem to be identical with those on the continents, with corresponding dependence on the climate. In oceanic islands the species—being immigrant—may occur in such habitats, which are not ecologically an optimum, because of the island environment peculiarities and restriction of the possibility of habitat preference. An immigrant species is forced by environmental pressure to occur in habitats that may not be too suitable for it, there being no more suitable habitats in the island. For this reason, widely eurytopic species seem to have better chances of successful establishment. A tropical climate with its corresponding influences on habitat requirements, seasonal occurrence, etc. of parasites seems to be also rather favourable.

– *Host specificity.* Climatic conditions of the island deeply influence the composition (establishment possibilities, etc.) of the flora and consequently also the composition of the aphid fauna. Their significance is different in different islands, although the occurrence of aphids in a given island is influenced by historical factors, spreading possibilities, etc.: the climate, through the flora occurrence, forms the presumption of environmental conditions development for an occurrence of certain aphid fauna in an island. This phenomenon then determines—besides specific features—the host range of a parasite species present in an island.

As mentioned above, the island fauna is in every case poorer than that of the neighbouring continent. This means, with respect to the host range of various parasite species (except monophagous species), that their host range must be restricted in an island area.

Each parasite species tries to get its place in the struggle for existence, in an island community as well. The pressure of the environment may be different in different islands. In some islands, where numerous aphid species exist and the parasite fauna is low in number of species, the pressure of the environment may not be so powerful as to force the parasite to parasitize new hosts. This might be true of some oceanic islands with a comparatively rich aphid fauna and poor parasite fauna.

In some continental islands (see below), the scheme of food chains is principally the same as in the neighbouring continents. Nevertheless, as these food chains are low in number due to the island conditions, some parasite species seem to try to cover other aphid species through interspecific competition, or to cover other aphid species that are not parasitized at all, in their host range in the given island.

Usually, and this is a phenomenon that generally corresponds to the aphid - parasite relationship in continents, there occurs in an island parasite fauna a certain species "in progress", which seems to be rather successful in including new hosts into its host specificity range in various parts of its distribution area. This is naturally different in different groups, depending on a number of factors. Island conditions may allow such species—due to the absence of some of their competitors—to parasitize certain new hosts.

Interspecific relations among the parasite species in continental islands seem to exhibit generally the same features as the relations in the continents. There may be some changes due to the partially different host aphid presence (see below: Cuba). In oceanic islands—due to the other fauna—there may appear other interspecific relations.

—Cuba. As mentioned above, the aphid parasite fauna of Cuba is not different as to its specific composition, being represented by Nearctic, Neotropical, and cosinopolitan parasite fauna elements. This is in obvious connection with its geographic position. Nevertheless, certain peculiarities may be recognized in the ecology of separate species, namely in their habitat requirements and host specificity. These peculiarities seem to be caused perhaps more by the inter-position of the island between the two regions (Nearctic, Neotropical) than by the island character of this area.

8 species and 2 species of unclear specific identity belonging to 7 genera have been established to occur in Cuba (STARÝ, 1967). This number is undoubtedly much less than the number of genera and species that occur in the south of the Nearctics.

The tropical climate of Cuba has no doubt caused certain changes in the habitat requirements in certain parasite species. Some of the parasites are there in more or less the same habitats as in their native home. This is obvious in *Pseudeplidrus neotropicalis*, which is connected with the tropical cloud forest zone. Somewhat striking, however, are the habitat requirements of the steppe species of the North American Steppes faunistic complex in Cuba. In their native home they are connected with the steppe landscape, being mostly parasites of the *Dactynotus*-, *Macrosiphum*-, etc., species, which are typical inhabitants of the steppe habitats. As is common in the steppe species, some of them may occur in the shady places in the steppe during the hot summer period. Nevertheless, the influence of a tropical climate has caused apparently certain other requirements on the habitats than those known to occur in the temperate zone and subtropics (penetrating of habitats from north to south). The two yearly periods—dry and wet—in the tropical climate of Cuba have no doubt

caused these changes. The aphids penetrate, following the ruderal places, etc., into the rain and cloud forest zone, where the conditions are the most suitable for them because of climatic and food reasons. There is almost a lack of the original steppe species in uncultivated savanna in Cuba, but we can find them occurring commonly in the tropical rain and cloud forest zone, as they follow the ruderals, clearings, river beds, etc. Some of the species, being more eurytopic and widely specialized, have penetrated into the close forest communities, too (*Lysiphlebus testaceipes*). All this has obviously been caused by the deep influence of the dry period in the lowland habitats while the submountains and mountains are less influenced, the conditions there being also suitable for both the aphids and parasites. If the influence of the dry period is not so deep, the aphids and parasites are probably more distributed also in the uncultivated savanna at that period. The cultivated savanna represents a somewhat changed habitat and some species such as *L. testaceipes* are often very common there too.

The isolation of a parasite species population in Cuba has apparently influenced its host range in some cases.

There is no doubt that except strictly specialized parasites, the number of host species is in every case much less than in the parasite's native home or non-island parts of its distribution area.

The general host range and island host range of parasites occurring in Cuba is shown by the following list:

Ephedrus incompletus: Distribution: Canada - Ont., U.S.A. - Florida, Ohio, Delaw., Tenn., west to Kansas, Hawaii; Cuba. Hosts: *Dactynotus erigeronensis*, U.S.A., Ohio; *Macrosiphum agrimonella* - Canada, *Lipaphis erysimi* - U.S.A., *Macrosiphum carpinicolens* - U.S.A. - Fla., *M. euphorbiae* - U.S.A. - Ohio, *M. liriiodendri* - U.S.A. - Ohio, *M. illini*, western N. America, Hawaii, *Metopolophium dirhodum*, *Myzus cerasi* - U.S.A., *Myzus persicae* - U.S.A. Hosts in Cuba: *Aulacorthum solani*, *Microparsus oliveri*, *Sitobium salviae*.

Pseudephedrus neotropicalis: Distribution: Cuba. Hosts: unknown in other areas except Cuba. Hosts in Cuba: *Neolizerius* sp.

Pauesia sp.: No detailed records on the species mentioned (mummies only.).

Aphidius floridaensis: Distribution: U.S.A. - Fla., Texas; West Indies (Cuba). Hosts: *Aphis gossypii* - U.S.A., *Dactynotus ambrosiae* - U.S.A., Florida. Hosts in Cuba: *Dactynotus ambrosiae*, *D. erigeronensis*.

Dicaetia rapae: Distribution: Cosmopolitan. Hosts: *Aphis abbreviata* - Canada, U.S.A. - Maine; *A. acanthi* - Spain; *A. ruminis* - Cyprus, *Brachycandus helichrysi* - Czechoslovakia; *Brachycolus noxus* - U.S.S.R. - Ukraine; *Brevicoryne brassicae* - Europe, America, Australia, N. Zealand, Africa, etc.; *Callaphis betulae* - Canada, *Dactynotus* sp. - Czechoslovakia; *Enceraphis betulae* - Canada; *Galiobium langei* - Czechoslovakia, Hayhurstia atriplicis - Canada, U.S.A., Czechoslovakia, U.S.S.R. - Eur. part; *Hyadaphis foeniculi* - Gr. Britain; *Lipaphis fritzmulleri* - Czechoslovakia; *L. pseudobrassicae* - U.S.A., *Macrosiphum euphorbiae* - Gr. Britain, Argentina; *Myzaphis berbiakoi* - U.S.S.R. - C. Asia; *Myzus persicae* - U.S.A., Hawaii, N. American States, Canada, Germany, Israel, U.S.S.R. - C. Asia, Japan; *Pterochloroides persicae* - Pakistan; *Rhopalosiphum maidis* - Morocco; *Schizaphis graminum* - U.S.S.R. - Ukraine, Argentina, Uruguay; *Schizaphis scirpi* - Czechoslovakia, Gr. Britain, *Sitobium* sp. - Czechoslovakia. Hosts in Cuba: *Brevicoryne brassicae*, *Lipaphis pseudobrassicae*, *Myzus persicae*.

Lysiphlebus testaceipes: Distribution: Nearctic region, some areas of Neotropical region, introduced into Hawaii. Hosts: *Anuraphis middletonii* - U.S.A.; *A. roseus* - U.S.A. - Maryland; *Aphis abbreviata* - U.S.A. - Maine, Canada; *A. agathariae* - U.S.A. - Calif., *A. bambusae* - U.S.A. - Alab.; *A. cerasifoliae* - U.S.A. - Idaho, Utah; *A. chrysanthemi* - U.S.A., Utah; *A. cornifoliae* - U.S.A., *A. craccivora* - U.S.A. - Ohio, Ariz., Calif., Hawaii; *A. cusatae* - U.S.A.; *A. fabae* - U.S.A. - Calif.; *A. farinosa* - U.S.A. - Ohio; *A. gossypii* - U.S.A. - Calif., Texas, Fla., Columbia, Ohio, Georg.,

Hawaii, Bermuda; Cuba; Puerto Rico; *A. gregalis* - U.S.A. - Idaho, *A. hederæ* - U.S.A.; *A. helianthi* - U.S.A. - Ohio, Utah, Calif., Canada; *A. heracleella* - U.S.A. - Idaho, Utah, Calif.; *A. labrum* - U.S.A. - Fla., *A. lutescens* - U.S.A. - Calif.; *A. malvifoliae* - U.S.A. - Va.; *A. mogilkei* - U.S.A. - Ohio; *A. neomexicana* - Canada; *A. neri* - Argentina; U.S.A. - Fla., Mexico, Bermuda, Puerto Rico; *A. oenotherae* - U.S.A. - Ohio; *A. oestlundii* - U.S.A. - Ohio; *A. phaceliae* - U.S.A. - Colo., *A. pomi* - U.S.A. - Calif.; *A. pseudohederae* - U.S.A. - Calif.; *A. ramosae* - U.S.A., *A. thamni* - U.S.A. - Fla., *A. rumicis* - U.S.A. - Iowa, Ohio, Idaho, N. Carol., Calif., Canada, Cuba; *A. spiraeola* - U.S.A. - Fla.; *A. spp.* - Canada, U.S.A. - Calif.; *Brevicoryne brassicae* - U.S.A., Cuba; *Cryptomyzus ribis* - U.S.A., Canada; *Dactynotus ambrosiae* - U.S.A. - Calif., *D. tanaetii* - U.S.A.; *Hysteronura setariae* - U.S.A., Puerto Rico, Cuba, Illinois *crebii* - U.S.A., *Lipaphis pseudobrassicae* - U.S.A., *Longiunguis sacchari*, U.S.A. - Hawaii, *Macrosiphum citrifolii* - U.S.A.; *M. cucurbitae* - U.S.A.; *M. rosae* - U.S.A., *Myzus crasi* - U.S.A.; Canada; *M. houghtoniensis* - U.S.A. - Ohio; *M. persicae* - U.S.A. - Ohio, Calif., Puerto Rico; *M. thamni* - U.S.A., *Neomyzus circumflexus* - U.S.A.; *Phorodon humuli* - U.S.A.; *Rhopalosiphum dianthi* - U.S.A.; *Rh. maidis* - U.S.A. - Color., Calif., La., Hawaii, Cuba, Puerto Rico, Mexico; *Rh. prunifoliae* - U.S.A.; *Siphia flava* - Puerto Rico; *Schizaphis graminum* - U.S.A. - Texas, Okla.; *Sitobium avenae* - U.S.A.; *S. graminum* - U.S.A.; *Toxoptera aurantii* - U.S.A. - Calif., Fla., Md., Puerto Rico. Hosts in Cuba: *Aphis coreopsidis*, *A. craccivora*, *A. gossypii*, *A. illinoisensis*, *A. neri*, *A. spiraeola*, *A. spp.*, *Brachycandus helichrysi*, *Carolinia cyperti*, *Dactynotus ambrosiae*, *D. crigeronensis*, *Hyperomyzus lactucae*, *H. communinensis*, *Hysteronura setariae*, *Myzus persicae*, *Pentaloma nigronervosa*, *Rhopalosiphoninus latysiphon*, *Rhopalosiphum maidis*, *Sitobium luteum*, *S. salviae*, *Toxoptera aurantii*.

Acanthocaudus tissoti: Distribution: U.S.A. - Fla., West Indies (Cuba). Hosts: *Dactynotus rudbeckiae*, Hosts in Cuba: *Dactynotus ambrosiae*.

Trioxys silvaticus: Distribution: Cuba. Hosts in Cuba: *Acyrtosiphon sp.*

Trioxys silvicola: Distribution: Cuba. Hosts in Cuba: *Aulacorthum solani*, *Sitobium luteum*.

Pressure of the environment, new host parasitization. The aphid parasite fauna of Cuba is without any doubt poor if compared with that of the neighbouring continents. If the host range of separate species found in Cuba is evaluated, it is obvious, namely in more specialized species, that they may find in Cuba only a part of the hosts they attack commonly in their native home. This is recognizable in the cases of *Acanthocaudus tissoti*, *Aphidius floridaensis*, *Ephedrus incompletus*, *Diaeretiella rapae*, etc. The more widely specialized species, such as *Lysiphlebus testaceipes*, have come into contact with the new hosts in the new (island) environment (cloud forest) and parasitized them, new hosts being then added to the host range of the parasite—the general host range of the species, however, remaining more numerous.

It really seems, and it is apparent in some species at least, that the restricted original host range forces the parasite to find new hosts in the island environment, such aphids being parasitized which would be probably omitted in the native home of the given parasite species, due to a sufficient number of other more suitable host aphid species present. Because of this restricted host range, the parasite is also forced to try to find new hosts in such environments, which would normally be omitted.

The above mentioned features, which have been recognized in the aphid parasite populations in Cuba, make these populations probably somewhat different from those of their native home or neighbouring continental areas. This consideration might be used in the biological control (exportation of some species, i.e. peculiar populations).

As to the interspecific competition, the taxonomic affinity of the hosts and their ecology have a different degree of importance in separate parasite species (see: Food specificity, and STARÝ, 1964). This is especially true in an island fauna. If the aphid parasites of Cuba in relation to the hosts are classified, the following conclusions seem

to be acceptable:

The aphid fauna, both as to the number of species and ecological groups, is much poorer than in the neighbouring continents. The same may be said of the parasites. When classifying the host-parasite relationship, it is obvious that the relation is generally the same as in the continents, only being more restricted, due to the peculiarities of the island fauna. Usually, only 1-2 parasite species are specialized to parasitism on certain groups (taxonomical and ecological) of the hosts, while the same or a similar group of hosts is usually attacked by a complex of species in the continents. Usually, a species is found which is very widely specialized and covers all the aphid species that are not attacked by a certain parasite species. The following examples may be mentioned:

(a) more strictly specialized parasites:

Aphidius floridaensis—*Dactynotus* sp.

Acanthocandus tissoti—*Dactynotus* sp.

Ephedrus incompletus—*Sitobium salviae*, *Microparsus olivei*, rarely *Anlacorthum solani*.

Diaretiella rapae—*Lipaphis pseudobrassicae*, *Brevicoryne brassicae*, *Myzus persicae*.

Pseudephedrus neotropicalis—*Neolizerius* sp.

Trioxys spp. and their hosts

(b) widely specialized species.

Lysiphlebus testaceipes—is a typical parasite of aphidine aphids, but it attacks also other aphid groups including *Dactynotus*, *Hyperomyzus*, etc. (interspecific competition).

The widely specialized parasite species usually cover all the non-parasitized host species because of the given island community equilibrium level. This is obvious from the classification of the host range of *Lysiphlebus testaceipes* in Cuba.

Similarly, in the hosts of separate species it is obvious they seem to infest in a higher degree the host species that have a similar ecology, the taxonomic affinity having no importance; *Ephedrus incompletus*—its main hosts are *Microparsus olivei*, and *Sitobium salviae*, while *Anlacorthum solani* is attacked only occasionally. Another case is that of *Trioxys silvicola* and its parasitization on *Anlacorthum solani* and *Sitobium luteum* in the cloud forest community. In this case, the species of the genus *Trioxys* are mostly strictly specialized and usually mentioned as examples of strict host specificity, the feature of parasitization of both the hosts mentioned with respect to their taxonomic relationship being rather remarkable.

Furthermore, it is obvious that every species—in accordance with the host specificity determining factors—has a certain main host or hosts, while certain hosts are clearly alternative or occasional. The main host occurrence here may be understood, among other points of view, as a result of successful interspecific competition in a restricted community. Examples:

Anlacorthum solani: In the cloud forest it is no doubt the main host of *Trioxys silvicola*; it is also attacked by *Ephedrus incompletus*. *Microparsus olivei* and *Sitobium salviae* are the main hosts of the latter species. Although *Ephedrus incompletus* may be classified as a phylogenetically more progressive species than the specialized *Trioxys silvicola* it is apparent it did not succeed in the interspecific competition in the case of *Anlacorthum solani* parasitization.

Lysiphlebus testaceipes: It is a widely specialized parasite, nevertheless, its main hosts belong to *Aphis* species and related groups. Being a progressive species, it either has covered all the groups that have no parasites in Cuba, or has attacked also other groups which have specialized parasites—in the latter case it seems, for the meantime, it has not been successful in this competition due to the percentage of parasitized aphids by both the competing species:

Dactynotus sp.: *Aphidius floridensis* and *Acanthocaudus tissoti* are the main parasites, *Lysiphlebus testaceipes* being an occasional parasite exclusively.

Sitobium salicis: *Ephedrus incompletus* is the main parasite, while *Lysiphlebus testaceipes* is an occasional parasite.

The classification of the mentioned relations, based on the host specificity comparison of the parasites both in their native home and in Cuba, is the necessary presumption when certain species have to be introduced into the island. The peculiarities of the island community equilibrium level, which are the result of a very long evolution, have to be kept in mind.

— *Hawaii*. The parasite fauna of Hawaii is a deeply oceanic type, consisting of members of various origin, which are not connected with certain floristic zones as to their spread to Hawaii, but they represent chance immigrants. Immigrants of the Nearctic origin, to a lesser degree species of the Far East or cosmopolitan species, may be found in Hawaii, besides two species purposely introduced by man.

8 species of the parasite have been established as occurring in Hawaii up till now. *Aphidius obscuripes*, *Ephedrus incompletus*, and *Monoclonus paulensis* are nearctic as to origin, *Aphidius gifuensis* is a Far East Asian species, *Diaeretiella rapae* is cosmopolitan. *Lysiphlebus testaceipes* is of Nearctic origin, *Aphidius smithi* is a species introduced originally in California and via insectary rearings to Hawaii and other countries.

No detailed data on the habitat requirements of the separate species are known. The parasites are mostly mentioned in connection with the parasitization of aphids of crops economically important, nevertheless, there are no records on their occurrence in the natural communities in which they surely occur as well, judging from the aphid fauna composition of Hawaii.

No detailed observations have been made up till now. The parasite species established in Hawaii have been usually mentioned as parasites of aphids they attack in their native home as well, thus being generally probable and does not mean anything about their biology in the island. Rather interesting and important records might probably be found if the complex research of the parasites with respect to the parasitism on aphids occurring in Hawaii would be undertaken.

— *ORIGIN AND RELATION TO OTHER TERRITORIES*. So far we may consider from the parasite material and records known to us, no peculiar insular fauna has originated in the separate islands. Nevertheless, today's populations—separated throughout a longer period from their related populations of the original area—might and probably do exhibit certain peculiarities (host preference, etc.).

The island fauna of parasites has been principally determined by the type of island. In the case of continental islands, there was sometimes a land connection with the mainland and floristic communities were identical at least in a certain period. The later separation of a part of the mainland as a separate island did not at first change the community, later certain changes developed to a various degree. Nevertheless, as to the parasites, according to our opinion, the continental islands are mostly situated not so far from the mainland as to prevent the continuous mainland fauna influence through aerial dispersal. The presence or absence of certain floristic communities determines basically the island fauna composition. In continental islands at least some parts of the original food chains may still be found and the relation to the mainland is apparent from the comparison of the fauna.

On the other hand, oceanic islands are just the contrary although certain floristic communities are often developed there, sometimes rich in number (Hawaii), they developed in an isolation and do not correspond to the mainland communities. Apparently they had originally no parasite fauna either. Only later some species immigrated to the island in various ways. The immigrant species mostly followed the

introduction and growing of various crops, so that the present day parasite fauna of oceanic islands is mostly connected with agriculture pest aphid fauna. This is apparent for instance from the specific composition of the fauna of Hawaii.

The origin of continental islands parasite fauna is easily recognizable when comparing the specific composition of the island fauna and that of the related continent. Natural communities are preferable due to their more or less original state, while cultivated crops fauna may exhibit secondary features.

Although the oceanic islands are characterized by their isolation, their fauna of parasites is composed of members of various origin, which form the peculiar oceanic island fauna. As the species of various origin select the best communities to live in, there are no typical faunistic complexes present, but there occurs a mixture of various species secondarily connected with various communities of the given oceanic island.

There are, however, certain groups of species predominant in separate island fauna. Being connected with agriculture, usually through the introduction of crops, etc., the parasites are naturally introduced from the same places as the crops.

For example, there is no doubt that in the case of Hawaii there is a predominant influence of Nearctic parasite fauna, to a lesser degree of the fauna of Far East Asia, which depends apparently on the trade activities of man.

Therefore, the oceanic islands are inhabited by a fauna of parasites, whose members represent primarily parasites of agriculture pest aphid species. Their composition depends on the country from which the crops are introduced.

—IMMIGRANTS. Judging from the comparison of the parasite fauna of islands and continents, aerial spread seems to be the most usual manner of parasite spread to the islands. As air streams have also the basic significance in aphid spread, this feature seems to be rather important in host and parasite relationship in spread. It does not mean naturally that the complete fauna of aphids and parasites will occur in an island and on a neighbouring continental area—all the cases known to us show that island fauna is in every case poorer than that of the continent. Aphid spread depends on the general directions of air streams, occurrence of certain host plant, seasonal occurrence, etc. A more complicated situation occurs in an aphid parasite, which has to find the aphid in the new environment. Naturally the widely specialized species seem to have a better chance of finding a host. Numerous examples of aerial spread may be recognized from the above mentioned review of islands, when the separate island faunas are compared with those of the neighbouring continents.

Man's activity, being connected with the transportation of various crops from one country to another, growing of crops in new areas, etc., has a great significance in the spread of parasites. Moreover, this activity of man has been occurring since the earliest periods of agriculture. From the point of view of our present day period we may subdivide man's activities with respect to aphid parasites spread into two following groups:

Accidental introduction. Accidental introduction seems to be the main source of aphid parasites in oceanic islands, i.e. in oceanic islands that are situated at far distances from the continents (Hawaii).

When we classify the fauna of parasites of Hawaii, it is apparent that the greatest part of the species, which are found there are parasites of common widely distributed pest aphids:

Acyrtosiphon pisum: *Aphidius obscuripes*

Brevicoryne brassicae: *Diacretiella rapae*

Macrosiphum granarium: *Aphidius obscuripes*

Macrosiphum rosae: *Ephedrus incompletus*

Myzus persicae: *Aphidius gifuensis*, *Diacretiella rapae*

Rhopalosiphum prunifoliae: *Aphidius obscuripes*
(Purposefully introduced and unclear species are not mentioned).

A nice example of an accidental introduction of a parasite by man to Hawaii has been mentioned by Hawaiian workers in 1931 (Notes and exhibitions, 1931): At the sessions of the Hawaiian Entomological Society they used to exhibit new immigrants, interesting and less known insects, etc. Once they exhibited three specimens of *Diaeretiella rapae*, which were reared from parasitized aphids found on a cauliflower from California, U.S.A. (apparently *Myzus persicae*, *Lipaphis pseudobrassicae*, or *Brevitoryne brassicae*—author's note). In this connection, they have noted this case as "It is a parasite that has been found in Hawaii for a long time, parasitizing aphids on cabbage. This incident illustrates how the parasite could have arrived here originally".

Purposeful introductions are a part of biological control activities. Two examples may be mentioned here, both of them being cases of introduction of parasites from Nearctic America (native or via insectaries) to Hawaii, the main task being to cover the gaps occurring due to lack of parasites of some pest aphids in this island:

Acyrtosiphon pisum: *Aphidius smithi* (introduced 1960).

Aphis craccivora

A. gossypii (introduced 1923, 1965)

A. nerii

Longinervis sacchari

Rhopalosiphum maidis

Lysiphlebus testaceipes

The comparison of islands—both continental and oceanic—has clearly shown that irrespective of the type of island the distance from a continent (source of fauna) seems to play an important role. The parasites may spread apparently with no difficulties over smaller distances from continents to islands, as is apparent from the case of the Canary Islands, Cuba, etc., and Bermuda, while greater distances—over oceans—seem to represent geographic barriers. This is apparent from the comparison of geographic distribution of the whole group (faunistic complexes, see: STARY 1967).

Three periods may theoretically be mentioned, in which a parasite may reach an island area: 1. Before the host aphid. Such a case is possible in an accidental introduction of exclusively mummified aphids, or in case of aerial transport. In this case, the specialized parasites cannot survive, while widely specialized parasites may find hosts and occur in the island. 2. Simultaneously with the host aphid. This case may be common, for example such as the one above mentioned (accidental introductions). Or, in another case, the simultaneous aerial transport of aphids and parasites through parasitized living (alate) aphids is possible as well. 3. After the host aphid spread. This seems to be the most common case. On the one hand, the aphids are numerous (alate spms.) and their successful spread seems to be more possible. The parasites following the aphids (air streams) may find host colonies then present in an island area and may parasitize them.

- NATURAL LIMITATION. The food chain aphids—natural enemies consists of many members as we can recognize from numerous samples taken in the field. Nevertheless, just from the evaluation of the samples, it is apparent that in almost no case can all the members of the given food chain be found in one sample. The separate species occurrence is influenced by a number of factors (environment, spread possibilities, seasonal history, etc.) The separate members substitute each other in the frame of the equilibrium level of the given community: If parasites are almost absent, the predators are more common and vice versa.

In island conditions the food chains exhibit a various degree of completeness. It is a general rule, that in continental islands they are of a similar scheme, being less, however, in number of their members if compared with the continent. In oceanic

islands they are mostly entirely original due to the different origin of their members (immigrants).

The same may be said generally about the specific composition of hyperparasites in islands. In continental islands they are less in number of species, nevertheless, they clearly belong to the continental fauna. The food chain is incomplete from the viewpoint of the continental fauna, nevertheless, one species or several species that occur in an island cover all the gaps caused by the absence of certain other species. This is a common rule in island fauna conditions, mentioned by various authors (SWEETMAN, 1936, etc.). For example, we ascertained only one group of hyperparasites of aphids, the chalcid *Pachyneuron* species during our research work in Cuba, while cynipids, proctotrupids and other chalcid flies are known as members of similar food chains in the neighbouring continents. In the oceanic islands the main principles are similar except that the hyperparasite fauna may be of various origin. We do not know any record with which we could compare the peculiarities of island-continent populations of hyperparasites. Judging from the host range of the hyperparasites, which seem to be more widely specialized than the primary parasites, the aphidiids, the island populations might probably exhibit less diversity when compared with continental populations.

As to the effectiveness of the hyperparasites, it is a general rule that the island species (continental islands namely), although being less in number, substitute the role of their absent relatives, so that a community equilibrium level is again relatively complete. According to our observations in Cuba, which support the earlier observations of some research workers on the effectiveness of hyperparasites in Hawaii, the hyperparasites of aphids were often extremely effective during certain periods of the year. The seasonal occurrence and effectiveness, the principal features, remained therefore similar to those in the neighbouring continents.

— ENDEMICIS AND RELICS. The criterion of endemics is relative from a certain point of view as it changes in dependence on time. As mentioned in the geographic distribution (STARÝ, 1967) it seems better to classify certain species as endemics of certain floristic zones than as endemics of certain continents or countries. For this reason, no endemics can be found in the island fauna of parasites. In continental islands the flora is similar to that of the mainland—at least as to the main floristic communities—, in oceanic islands there is a peculiar flora, which has developed independently, the parasite species being immigrant. The parasite species, described originally from an island, either oceanic or continental, will, sooner or later, be found in a continent, too. A number of such cases can be mentioned (see: Far East Asian fauna, British Isles, etc.).

According to our studies on the geographic distribution of parasites and its development, we do not recognize any relics of a certain area or country, but relics of a certain floristic zone. For this reason, any identification of a parasite species as a relic of an island is presumed to be incorrect.

This problem of parasite relics in islands has not been dealt with sufficiently. The single record known seems that of MACKAUER (1962), according to which "the occurrence of *Trioxys panmonicus* in the Canary islands cannot be connected with any record from Central Europe, the Mediterranean subregion, or from the Middle East, though the host aphid is distributed throughout Europe and *Artemisia* sp. are common plants in the Mediterranean area." We have classified MACKAUER's opinion that *Tr. panmonicus* is a faunal relic in the Canarian from the warm tertiary period as being rather doubtful. The parasite, which has been found up till now in Germany and the Danubian lowlands (south eastern Czechoslovakia, Hungary), is a member of the Eurasian Steppes faunistic complex. This complex is rather numerous

covering also the parasites of the *Dactynotus*, etc. aphids, to which group *Tr. pannonicus* belongs as well as a parasite of *Titanosiphon artemisiae*. These species, besides other areas of Eurasia, have been widely and commonly distributed over the Mediterranean. *Artemisia canipestris*, the host plant of the aphid, has been mentioned as an example of seed dispersal by cattle in the case of the Canaries by RIDLEY (1959). For this reason it can be supposed that the appearance of such weed plants in the Canaries may be expected to be soon followed by the aphids (and parasites) via aerial plankton dispersal. This has apparently been the way of *Tr. pannonicus* as well, the species being more widely distributed than the recent records have shown. In no case can we support MACKAUER's opinion keeping the occurrence of the parasite in the Canaries as an indication that a former land connection with continental Europe existed. Although the floristic records (RIDLEY, 1959) have shown the apparent land connection of the Canaries in the past, to apply the occurrence of such dispersable forms as aphids and apparently also the parasites for such a task seems to be unjustified in this case.

—VICARIANCY. According to our studies there has not been an original fauna developed in various islands, hence no taxonomical vicariants can be found in island faunas.

In continental islands—due to the same although less numerous fauna—there may be the same ecological vicariants as in various separate faunistic complexes in the mainland (see Geographic distribution, STARÝ, 1967). In oceanic islands, ecological vicariants can be found there, for example, among the parasites of widely distributed aphid pest species.

—FAUNAL CONNECTIONS. As we have shown in geographic distribution research (STARÝ, 1967), very poor connections exist between the separate continents. This is recognizable from the development of separate floristic zones, which have been deeply influenced through the geological history of the earth. The aphidids, being dependent on floristic zones in the main features in their distribution, have been influenced in a corresponding way.

In the existing or probable connections, islands have played a certain role, nevertheless, only three apparent cases may be mentioned:

—British Isles. Although the British Isles may be generally classified as a part of continental Europe as to their fauna, they have a position which is somewhat similar to that of Iceland. Although there are members of several faunistic complexes distributed over the British Isles, the occurrence of the members of the Holarctic Forest Tundra faunistic complex is most important with respect to the spread of the species via Iceland to N. America. There is no doubt about the importance of the British Isles as a part of the migration route of the Forest-tundra faunistic elements to N. America.

—Iceland. This island has been important in the spread of holarctic forest-tundra faunistic elements from Europe to Nearctic America. Whether it was in the period of land-bridge connections, etc., we cannot say as there are various opinions on the existence of such a bridge at all. Nevertheless, there is no doubt that identical forms may be found in the boreal areas of Europe, on the British Isles, Iceland, in the southern part of Greenland, and at least in the northern parts of Nearctic America.

The role of Iceland as a distinct where parasite fauna has occurred during the period of its spread is apparent. There are, besides the Holarctic Forest Tundra faunistic complex elements (*Aphidius angulatus*, *Trioxys compressicornis*, etc.) distributed some members (*Ephedrus plagiator*, *Praon volucre*) of the European Deciduous Forest faunistic complex. Such species are widely distributed and penetrate to the northern areas of present day Europe as well.

-Cuba. The comparison of aphid and parasite fauna of the southern parts of N. America, C. America, the West Indies and northern parts of S. America has shown that this island as well as some other islands of the West Indies (Puerto Rico) have probably played a certain role in the spread of faunistic elements from the north to the south. There is no doubt of the influence of both N. and S. American fauna on the fauna of Cuba. Nevertheless, the distribution of *Lysiphlebus testaceipes*—a species of clearly Nearctic origin—to the south shows such a kind of migration route. Similarly, the spread of *Aphis spiraeicola* to the tropics, a matter of the present day, more or less, is also an indication of the existence of such a migration route "Florida - West Indies - S. America". As to other research, there is almost entire lack of knowledge of the parasites of the northern parts of S. America, so that elucidation of those connections has to be left as a problem for further research.

For comparison, the example of an oceanic island—such as Hawaii—might be mentioned. As already mentioned, the presence of certain species in this island shows certain influences of faunas through man's agency. Thus, it may be possible that similar "route" i.e. directions of faunal influences via man's agency occur in other cases, too. Nevertheless, such routes occur today all over the world, although in earlier times apparently there was a better possibility for the spread of faunas in such a way as mentioned, as today strict quarantine measures have been mostly accepted in various countries.

REFERENCES. 2, 12-15, 45, 60-1, 62, 86, 116, 126, 128, 164, 185, 219, 223, 233, 317, 336, 348, 430-7, 451, 467, 472, 475, 504, 528-30, 544, 567, 593, 602-4, 621, 658, 660-1, 669, 681, 682, 691, 696, 798, 829-36, 841-3, 880, 881, 896, 911, 944, 946, 1006, 1023, 1047, 1086, 1127-30, 1134, 1164-75, 1183-4, 1215-8, 1224-5, 1262, 1264, 1268, 1323-4, 1328, 1336-7.

Biological Control

Immigrant pests are generally classified as more useful objects for biological attempts than the indigenous pest species.

In the case of the introduction and establishment of a pest aphid in a new country, the indigenous parasites are usually left behind. The adaptation of indigenous parasites may be a slow process. On the one hand, chemicals are applied to control pest outbreaks, on the other hand, search for natural enemies is organised, mainly with the effort of obtaining parasites from the countries of pest origin and establish them in the given country where the pest has gained a new foothold.

In our opinion, this is only one part of the introduction possibilities. The above mentioned generally followed process in search for parasites has been widely discussed by BARTLETT and V. D. BOSCH (in DEBACH & SCHLINGER, 1964). These authors have also recognized the general acceptance of the above mentioned primary rule: natural enemies capable of attacking and destroying the pest species in its new home are best sought in the land of the pest origin. Nevertheless, they have widely and critically commented various other principles connected with foreign exploration of parasites (natural enemies). Exclusion of areas other than the native habitat of the pest species cannot be categorically accepted: search for natural enemies can be profitably extended to areas other than the native home of the pest species. Introduced pest species, too, may acquire effective natural enemies from allied native insect hosts. In the importation of exotic beneficial arthropods it is generally felt that the more similar the climate of the native home and that of the land of introduction, the greater the probability of natural enemy establishment and success. They have

mentioned, however, that it is almost impossible to predict exactly how an imported species will respond to a new climatic environment. With respect to the activity of a parasite in the distribution area of the pest, the importance for search and collection of parasites all over the area of host distribution are stressed; importation of several parasite species is recommended to cover all the diverse habitats of the pest; collection in areas of a diverse climate is useful—the more entomophagous species imported and the greater their range of climatic adaptation, the greater will be the expected geographical extent of biological control in the land of destination.

Owing to the scope of the compendium mentioned (DEBACH & SCHLINGER, 1964), which has at first to throw general ideas on biological control as a whole, numerous illustrative examples being mentioned, we have decided to check the principles of search and introduction of parasites from the viewpoint of our book, to show mainly the importance and necessity of approach to search and introduction from the standpoint of geographic distribution of parasites (general rules, see: Biological control).

The features of geographic distribution of parasites are very helpful when a parasite introduction program is elaborated: The zonal dependence in parasite distribution, the role of geological history, host range of parasite and its role in geographic distribution, seem to be most important and valuable.

— PARASITE FAUNA OF A GIVEN AREA. The following possibilities in aphid-parasite relationship may be recognized with respect to the given area:

A. No aphidid parasite in the given area. The pest aphid may be free of parasites in the given area only, or it may be free of aphidid parasites altogether in the case that it belongs to a group which is completely omitted by aphidid parasites (Adelgoid aphids, etc.).

B. Indigenous parasites.

(a) The newly introduced aphid is taxonomically and morphologically related to the host of the indigenous parasites in the given type of habitat. In this case it is to be expected that the indigenous parasites of hosts that are related to the newly introduced aphid will also attack this aphid. It seems to be obvious that the parasitization of a newly introduced aphid will also depend on the number and effectiveness of the indigenous parasite species present. In case of the presence of a relatively high number of parasite species, it is more probable that one of the indigenous species will also attack and successfully parasitize the newly introduced host in the given community, especially if the new host species is related both taxonomically and morphologically to its indigenous host aphid species. Many *Aphis*-like aphids can be mentioned as an example. Various degree of adaptation of the native parasites may naturally be recognized (Example: *Chromaphys juglandicola*, indigenous and introduced parasites in Nearctic America).

(b) The newly introduced aphid is too far from the specificity range of indigenous parasites. In this case the aphid may be left unparasitized and a possible outbreak on cultivated plants may be expected. Example: *Therioaphys trifolii* in California, etc.).

C. Parasites introduced accidentally and simultaneously with the aphid in the new country. Example: *Brevicoryne brassicae* and its cosmopolitan parasite *Diaeretiella rapae*.

Because of the factors that influence the spread of aphids (air streams, human agency, etc.), their indigenous parasites may spread in a similar way. Examples might be mentioned when an aphid species and strictly specialized parasites were found in isolated islands, far from their native home. With respect to the accidental introduction the following possibilities may be recognized:

(a) Parasites are effective species

a. In the former, but need not be in the new country.

b. Both in the former and in the new country. In this case the aphid may also be held below economic importance level in the new country.

(b) Parasites are not effective species.

a. In the former country, but need not be in the new country.

b. Both in the former and in the new country.

D. Introduced parasites—purposeful introduction for biological control. The parasites are introduced into a given country in case:

(a) No parasites are present.

(b) No effective parasites (indigenous or simultaneously introduced present).

(c) Effective parasites present, the aphid because of seasonal history etc., is not controlled in a certain part of the season (pest).

(d) Effective parasites present, the pest aphid controlled on the given crop under economic injury level; the aphid causes also other damage (virus vector) on other crops, though being less in number.

—APHID SPREAD. The aphids may spread in a natural way or they may be introduced. In both cases the economic importance can be the same (Figs. 282-290).

Nevertheless, in case that an aphid species spreads gradually enlarging its area of distribution, the parasites usually follow it, they may or may not exhibit the same or similar features as in the original area. Sometimes, the aphid area may be relatively smaller than the area of its parasites. For example, in Nearctic America (the general distribution area of the aphid is not mentioned) the area of *Lysiphlebus testaceipes* is more widespread than that of *Aphis spiraeicola*. The parasite covers the whole Nearctic America, C. America, West Indies and some areas of S. America as well, while the aphid spread to the tropics probably only in the thirties, being naturally found to be attacked by the parasite in all the new countries.

The spreading aphid may have a different economic importance too. *Aphis spiraeicola* has become an important pest of Citrus growing areas, and a widely specialized pest in tropical areas, being, however, not classified as a serious pest in the north. Aphid outbreaks known in case of the aphid are seemingly caused by local low efficiency of the parasites, not by their host specificity range.

If the aphid species spreads out of the distribution area of its parasite, there is a possibility of serious and almost perpetual occurrence and aphid outbreak in the new territories, if other factors (climate, host plants, etc.) permit. Just the overrunning of a geographic barrier (ocean), usually due to man's activity, may result in outbreaks of pest aphids introduced. A number of introduced pest aphids into Nearctic America may be mentioned as examples (*Therioaphis trifolii*, *Acyrtosiphon pisum*, *Chromaphis inglandicola*, etc.).

The spreading aphid species comes sooner or later into contact with certain faunistic complexes of parasites. We have selected several remarkable examples to illustrate such types of aphid spread in relation to parasites. Naturally, the examples mentioned cannot cover the extreme variability of aphids as to their distribution patterns and history.

1. *Eriosoma lanigerum* (Fig. 282)

Being N.-American in origin, it has spread almost all over the world. Aphidid parasites of this aphid have been unknown from the U.S.A. up till now. The aphid was introduced at the end of the 18th and at the beginning of the 19th century to Europe, apparently with no aphidid parasites. In 1926 WATERSTON described a new species of *Praon* parasite from Gr. Britain, which was originally mentioned as a parasite of *E. lanigerum*. Nevertheless, further research of the aphidid parasites in Europe has shown that the parasite—*Aecopraon lepellei*—is a typical species parasitizing the *Schizoneura* and *Eriosoma* aphids which are responsible for producing

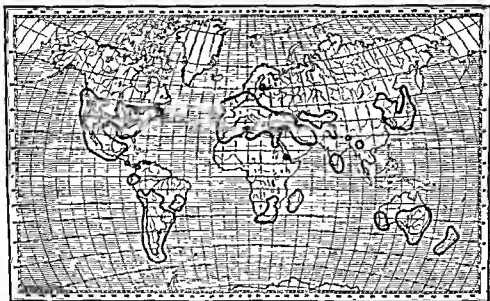


Fig. 282. Distribution of *Eriosoma lanigerum* (after Distribution Maps of Insect Pests, A, 17. Commonwealth Inst. of Entomology).

various galls in *Ulmus* in the spring months. There can be no doubt, therefore, that the parasite adapted very early to parasitism of the *E. lanigerum* aphid, as it was a species related to its hosts both taxonomically and perhaps ecologically as well, although not being a gall aphid; nevertheless, the strong wax cover and character of the colonies were apparently useful for the parasite. This seems to be mentioned as an example of how an aphid may become an accidentally introduced member of new communities, and how the native parasites may become adapted to it. It is necessary to add that we have been unable to rear the parasite mentioned from *E. lanigerum* in other localities in Europe, so that the parasitism does not seem to be quite common in Europe as yet. Nevertheless, the original material of WATERSTON is well preserved in the British Museum collections, so that a misunderstanding—due to the apparent distinguishing characters as well—is almost excluded.

2. *Therioaphis trifolii* (Fig. 283)

This aphid has occurred primarily in the semi-desert and steppe zone of the Old World. Recently, it was introduced into the U.S.A. and has become a serious pest. Because of the taxonomic isolation and absence of similar parasites in the U.S.A., California, it soon caused heavy damage to alfalfa. Today the aphid is successfully controlled by the aphid parasites—besides other natural enemies—that were introduced from the Old World, the conditions, therefore, seemingly being similar to those of the Old World.

3. *Toxoptera citricidus* (Fig. 284)

This aphid is primarily connected with the tropical rain forest, attached to the tropical belt. It has not followed the Citrus growth into the subtropical countries, as for example *T. aurantii* has, but it is a serious pest—being a virus vector namely—of Citrus in tropical countries. Aphid parasites of this aphid are almost unknown. This is probably due to the poor level of research, as the aphid does not seem to represent an isolated group. Further research and eventual unnatural host propagation is necessary.

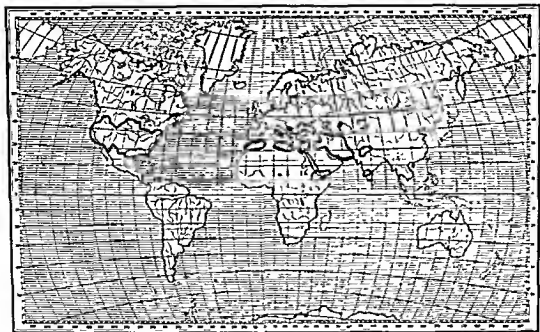


Fig. 283. Distribution of *Therioaphis trifolii* (= *maculata* Bckt.) (after Distribution Maps of Insect Pests, A, 126. Commonwealth Inst. of Entomology).

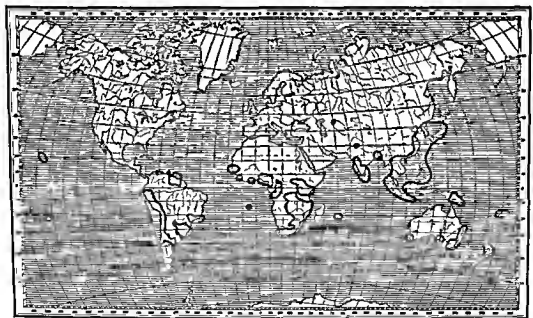


Fig. 284. Distribution of *Toxoptera citricidus* (after Distribution Maps of Insect Pests A, 132. Commonwealth Inst. of Entomology).

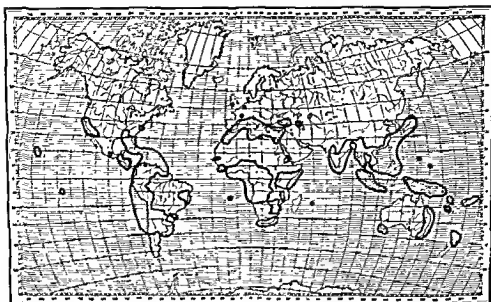


Fig. 285. Distribution of *Toxoptera aurantii* (after Distribution Maps of Insect Pests, A, 131. Commonwealth Inst. of Entomology).

4. *Toxoptera aurantii* (Fig. 285).

The aphid is attached primarily to the tropical districts of south-eastern Asia. Contrary to *T. citricidius* it has followed the Citrus and become established in quite a number of both subtropical and tropical countries. It is a typical pan-sub-tropical and -tropical pest.

It is an illustrative example of the application of faunistic complexes classification to biological control praxis (Fig. 290). Being primarily a south-eastern Asian aphid species, and having spread to other parts of the world, it is attacked by various parasite complexes, besides its native parasite complex in south-east Asia, in southern Europe, Nearctic America, S. America, etc., the possibilities of mutual introductions of parasites being wide. Moreover, its parasites attack a number of other aphids too, so that the biological control may cover several pest and other aphids simultaneously.

5. *Aphis gossypii* (Fig. 286).

It is a member of a very numerous aphid genus *Aphis*, being distributed in various countries of temperate, subtropical and tropical climatic belts. It is attacked by various parasite complexes in various parts of the world. Again, there is a wide possibility of the application of research of faunistic complexes of parasites. Similarly as in *Toxoptera aurantii*, its parasites attack also other pest aphids of the Aphidina group.

6. *Brevicoryne brassicae* (Fig. 287)

This is a type of a typical cosmopolitan aphid that was introduced or spread accidentally almost to all countries. It is a Myzine aphid, its relatives being parasitized by many parasite species. Due probably to its ecology (wax covers, etc.), the aphid is attacked by comparatively few aphid parasites, *Diaeretiella rapae* being the most common and most widely distributed. In this case, the influence of faunistic complexes is not so remarkable. Although the aphid is attacked by various parasites in different countries, this seems to be more a matter of host preference.

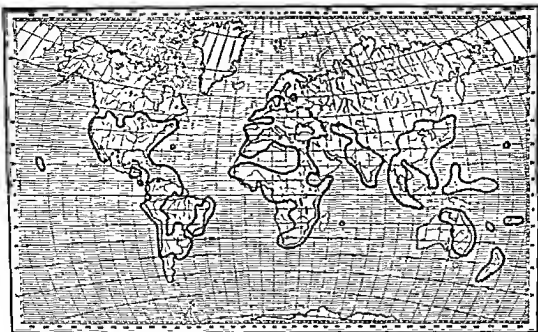


Fig. 286. Distribution of *Aphis gossypii* (after Distribution Maps of Insect Pests, A, 18. Commonwealth Inst. of Entomology).

7. *Rhopalosiphum maidis* (Fig. 288) (seasonal spread northwards).

In this case, we do not want to deal with the pan-sub- and pan-tropical distribution of the aphid, which seems to exhibit similar host - parasite complex relations as e.g. *Aphis gossypii*, etc. *Rhopalosiphum maidis*, as mentioned by various authors (see MÜLLER, 1966), is limited to a moderate-tropical zone, being unable to overwinter in northern areas with severe winter conditions; however, in spring mass dispersal of aphids to the north had been observed, heavy infestation of Indian corn (*Zea mays*) and damage being caused during the season; nevertheless, the aphids did not overwinter, new mass flight following the next spring from southern areas. This means that *Rh. maidis* might seasonally fall under the influence of parasites in the northern areas, the parasites belonging possibly to other complexes than the parasites in the south. Unfortunately, we have no respective records on parasites of the aphid in northern-southern areas of Europe and Nearctic America.

Therioaphis trifolii was a similar example, nevertheless, it is mentioned as exhibiting more adaptive features and overwintering (some populations) in egg stage in the northern areas of the U.S.A. (see: *Therioaphis trifolii* biol. control).

- VARIATION IN PEST APHID FAUNA. It is generally known that the composition of aphid pests of separate crops may vary in dependence on the area. There are cosmopolitan species, or species restricted to a climatic belt—tropicopolis, subtropicopolis, etc., besides area-restricted hosts.

The variation of pest aphid fauna correspondingly conditions the variation of composition and significance of separate parasite species in various areas.

Practically each crop represents a separate case, no generalization is possible. Aphid pests attacking cotton, sugar cane, citrus, corn, vegetables, fruit trees, etc., might be mentioned as rich sources of information and illustration.

Furthermore, the same pest species can be of different economic significance in various areas. The geographically dependent role of aphids as pests is important

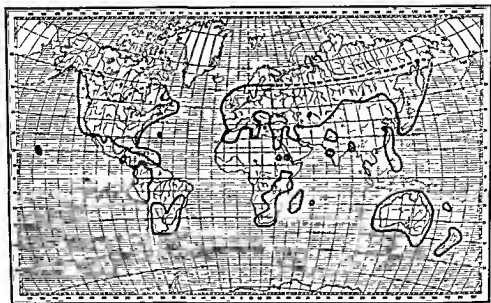


Fig. 287. Distribution of *Brevicoryne brassicae* (after Distribution Maps of Insect Pests, A, 37. Commonwealth Inst. of Entomology).

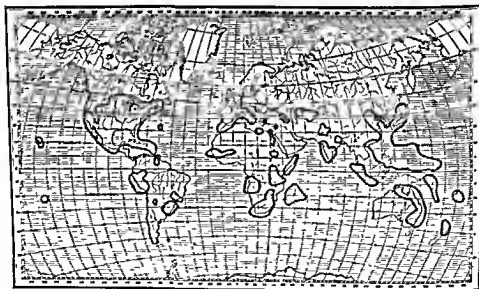


Fig. 288. Distribution of *Rhopalosiphum maidis* (after Distribution Maps of Insect Pests, A, 67. Commonwealth Inst. of Entomology).

with respect to the role of parasites as well. The parasites may play a different role as agents in limiting or controlling certain pest aphids in various parts of their distribution area. All the parasites that attack a given pest, disregarding the role of the aphid in a given area, must be taken into consideration. If an aphid is not a pest in a given district, this may be due either to generally unfavourable environmental conditions for the aphid in the given district, or due to the successful limitation of this aphid by natural enemies (incl. parasites). Such a situation must be evaluated at least generally, when a biological control program is elaborated.

— SIGNIFICANCE. The classification of faunistic complexes of parasites is rather important for the biological control of aphids, in the initial phases of the biological control program for example. In the case of a widely distributed aphid (Fig. 289) it is necessary to bear in mind that this aphid has its native home (country O), where it is attacked by indigenous parasite complexes. But, because of the spread, the aphid gradually occurs in other territories and thus comes into touch with other faunistic complexes of parasites (country A). If it is related to aphid species of country "A", it is probable that it will be attacked by the indigenous parasites of country "A". Thus, the cosmopolitan aphid can be attacked by different parasite complexes in various parts of its distribution area. Several cases are known, for example: *Aphis spiraeicola*, *A. craccivora*, *A. gossypii*, *Toxoptera aurantii* (Fig. 290). Knowing the faunistic complexes and the taxonomy and ecology of the pest aphid, we can either presume which species will attack the pest aphid in its new distribution area, or introduce such a species from various countries and use them in an unnatural host propagation program.

The knowledge of faunistic complexes of parasites, peculiarities of their distribution, permit the elaboration of introductory aphid control in such areas where the pest aphids damage various crops, and where the effectiveness of indigenous parasites is very low or where they are almost absent. In island communities, in oceanic islands namely, such circumstances can be found. Moreover, the accidental development of the composition of host aphid-parasites in (oceanic) islands clearly shows that the main difference between oceanic islands and continental faunas are food chains composed of members of various origin which are not found in the continents. Therefore, similar artificial creation of food chains can be the task of biological control work, nevertheless, contrary to incidental creation, they must be composed of carefully selected parasite species. A similar task for biological control work seems to occur in "ecological" islands, such as may represent extensive crop plantations in newly cultivated desert areas, etc. According to PEARSON (1958), e.g., the major pest aphid of cotton plantations in tropical Africa is *Aphis gossypii*, only one *Aphidius* sp. occurring rarely as its parasite in these districts, although the aphid is heavily parasitized by certain parasites in other cotton growing areas, e.g. in Nearctic America. A biological control program should result in selection and introduction of effective species from suitable districts (e.g. introduction of *Lysiphlebus testaceipes* from the Nearctics). An artificial food chain is also created when introducing foreign parasite species to control indigenous pest aphids in a given country. Similarly, if an introduced pest aphid species is attacked by indigenous parasites, new (accidental) food chains appear, being possibly completed by purposeful introduction of some foreign parasites (e.g. *Acyrtosiphon pisum* in Nearctic America, its indigenous parasites in this area and introduction of *Aphidius smithi* from India to Nearctic America). Introduction of foreign parasite species (from the pest's native country) to control an introduced pest in a new country does not represent a creation of a new chain, but a transferring of an existing and known chain to a new area (e.g. *Therioaphis trifolii* in Nearctic America and introduced parasites *Trioxys complanatus* and *Praon exoletum*).

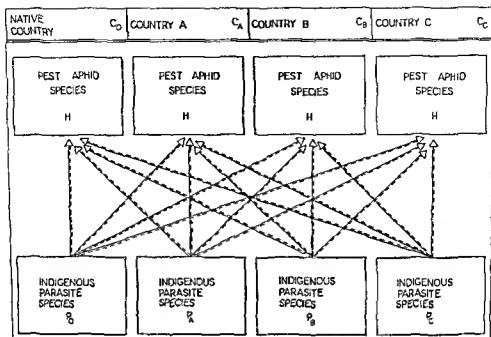


Fig. 289. Parasite introduction scheme.

- BASIC RULES. The influence of geological periods on the floras and aphid and parasite faunas has caused the formation of separate faunistic complexes of aphidid parasites of today.

Every parasite species has to be classified as a member of a certain faunistic complex, thus enabling certain theoretical conclusions as to its spread and occurrence.

Parasites are primarily attached to certain floristic zones, not to continents.

Vertical zonation of parasite corresponds to vertical zonation of separate floristic formations.

Classification of faunistic complexes and their mutual relations enable the identification of the zone of possible distribution which is of great importance for the selection of parasite species for introduction.

The microclimate is rather important. It determines the distribution of parasites in the limits of a given floristic zone.

The systematical and ecological vicariance of species of different faunistic complexes shows the importance of research of centers of origin, centers of distribution, host ecology, etc., for the classification of phylogeny of parasites and derivate classification of the separate species for biological control purposes.

The Far East, Europe, Nearctic America, are the three known main centers of parasite group development. Of these, the Far East is the most ancient. The Far East and Europe are connected, the Nearctic fauna is isolated except for the circumpolar Holarctic Forest Tundra zone, the elements of which apparently invaded the Nearctics from Europe via Iceland, being followed (possibly) by some species of the European Deciduous Forest complex.

Responses to the influence of changes in environmental conditions can be different in hosts and parasites. No phylogeny parallelism rule can be applied except in some cases. Taxonomic, phylogenetic, ecological classification of the host, similarly as its geographic distribution classification are the basic principles.

The history of spread of the crop may be useful.

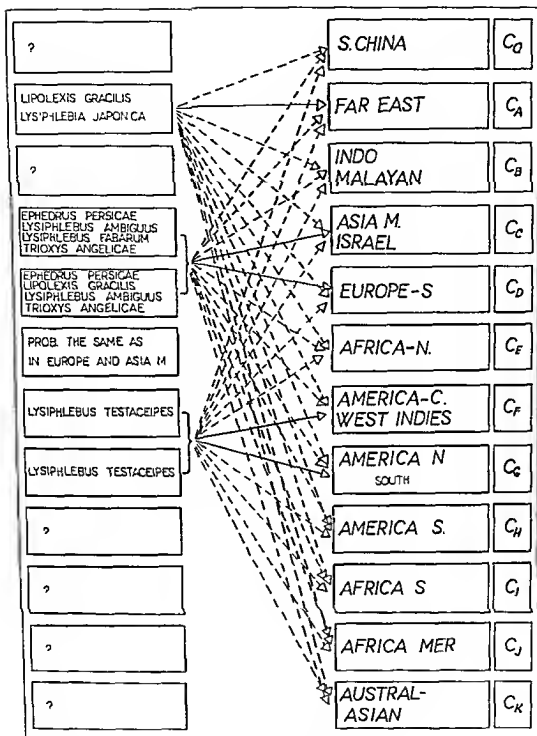


Fig. 290. Distribution of *Toxoptera aurantii* and its parasites.

The introduction of the parasite from the "native home" of the pest for the biological control of the given pest in a new territory is only a part of the introductory possibilities.

Parasites of separate faunistic complexes that attack the pest aphid in various parts of its distribution area may be of the same or greater importance than the primary indigenous parasites.

The aphid pest comes into contact with various faunistic complexes of parasites in various parts of its distribution area.

Parasites that are little effective in their native country may be very effective as introduced species.

Widely specialized parasite species are rather suitable for introduction. They are on the one hand usually more plastic ecologically (wide host range, various habitats), on the other hand they usually successfully attack other hosts in the new environment in case of the pest aphid host absence.

The knowledge of habitat in different species is very important. The species has to be introduced to the same or at least to a similar habitat as in the country of origin. The knowledge of habitat is useful for the distinguishing of the sibling species.

Parasites occurring in coniferous and deciduous forests represent primarily strictly different complexes. Parasites of deciduous forest aphids have partly strong phylogenetical connections with the steppe species, the fauna of today is, however, different.

Deciduous forest complex parasites may penetrate far to the steppe zone following the deciduous forest elements.

Tropical conditions are specific, both because of parasite phylogeny and occurrence.

Generally, species of the temperate and subtropical areas may be useful in biological control of pest aphids in the tropics (pan-tropical and cosmopolitan pest aphids).

The spread of an aphid from the distribution area is especially dangerous in case of old and isolated groups of aphids with specialized parasite complexes. In case of a member of a large and numerous aphid group, the possibility of successful adaptation of members of faunistic complexes of parasites in the new district of aphid area is more probable.

North-South introduction is recommended.

In widely specialized parasite species that are usually widely distributed, it is recommended to select the populations of a similar climatic belt which are also adapted to the aphid or its close relatives.

In the area of distribution the separate parasite populations may exhibit characteristic features (seasonal arrested states in development, parthenogenesis). Careful selection is necessary, the mentioned peculiarities may have a positive or an adverse role in biological control praxis.

Seasonal dependence. Population of parasites taken in different seasons may be different as to their responses to temperature and relative humidity conditions.

It is useful to unify the biological control of several pest aphids simultaneously. The aphid may be a pest as a sucking species in one crop, being a virus vector in another, with various degrees of importance. A multilateral aphid control concept has to be applied.

The parasite has to be introduced both in the natural community where the pest occurs and in the field conditions.

The classification of faunistic complexes and host specificity knowledge of the parasite enable the elaboration of its probable response to the new environment (spread, occurrence, alternative hosts), although no definite answer can be given before the parasite is really successfully established in the new environment.

Biological control of aphids in oceanic islands, due to the tropical climate, composition of aphid fauna, is a rather suitable subject for biological control of aphids by parasites.

Arid zone problems. The irrigation of arid zone districts causes a change of climate to a certain degree. It is probable that species of the temperate zone might be successfully established here as well.

- **EXAMPLES.** It seems necessary to add that the evaluation of inter-relationship of the separate pests to the environment—both to wild plants and cultivated crops—has indirectly caused our elaboration of the Multilateral aphid control concept. As a result, biological control of an aphid pest on several crops simultaneously seems to be possible, similarly as biological control of several pest aphids by a single parasite species. In some cases in strictly specialized pests and strictly specialized parasites the viewpoint of the crops and that of the pest may be identical, for example alfalfa and *Therioaphis trifolii*.

Nevertheless, further details on these aspects being mentioned in the biological control chapter, the initial stages of the biological control program remain the same, and it is just the purpose of this paragraph to show the significance of knowledge of the geographic distribution of parasites in the biological control program.

- **Citrus.** It is generally believed that all the various species of Citrus are native mostly in the subtropical and tropical regions of south-east Asia, from where they have spread through man's agency to other districts of their present distribution area. The following main pest aphid species were found to attack Citrus: *Aphis craccivora*, *A. spiraeicola*, *A. gossypii*, *Myzus persicae*, *Toxoptera aurantii*, *T. citricidus*.

The biological features of Citrus determine also the infestation by the pest aphids. It is preferred mostly by a forest-type habitat inhabiting species, such as *Toxoptera aurantii* and *T. citricidus*, who seem to be native pests of Citrus in its home, south-east Asia, while the other aphids, being apparently adapted secondarily to tropical conditions, attack Citrus in the same way as other crops.

Aphis craccivora. Its origin is unclear, probably steppe areas of the Palearctic region. It is widely distributed, almost cosmopolitan. Habitat: Temperate to subtropical zone, it prefers habitats of steppe type, being common in fields, penetrating to forest-steppe and farmland, parks, etc. Everywhere in the tropics, from savannah to tropical rain forest. Host range: It prefers leguminous crops, but attacks a number of other crops and plants as well. Classification of parasite species-faunistic complexes: Far Eastern Deciduous Forest - *Ephedrus persicae*, European Deciduous Forest - *Lysiphlebus ambiguus*, *Praon abjectum*, *Pr. volucre*, *Trioxys angelicae*, Eurasian Steppes - *Lipolexis gracilis*, *Lysiphlebus fabarum*, *Trioxys aculephae*, Nearctic Steppes - *Lysiphlebus testaceipes*. Selection of species to introduce: *Lipolexis gracilis*, *Lysiphlebus ambiguus*, *L. fabarum*, *L. testaceipes*, *Praon abjectum*, *Trioxys aculephae*, *Tr. angelicae*. Unnatural host propagation recommendations: *Lysiphlebia japonica*, *Ephedrus plagiator*.

Aphis gossypii. Its origin is unclear, probably steppe areas of the Palearctic region. Almost cosmopolitan, with the exception of the northern parts. Habitat: widely eurytopic species, in the temperate and subtropical zone in steppe type habitats. Host range: Widely polyphagous. Classification of parasite species - faunistic complexes: Far Eastern Deciduous Forest - *Ephedrus persicae*, *E. plagiator*, *Lysiphlebia japonica*, *Aphidius gifuensis*, Eurasian Steppes - *Lipolexis gracilis*, *Lysiphlebus fabarum*, Nearctic Steppes - *Lysiphlebus testaceipes*. Selection of species to introduce: *Aphidius gifuensis*, *Lipolexis gracilis*, *Lysiphlebus fabarum*, *L. testaceipes*. Unnatural host propagation - recommendations: *Trioxys aculephae*, *Lysiphlebus ambiguus*.

Aphis spiraeicola. Its origin is not clear, probably Nearctic America or the Far East. Distribution: C. and S. Europe, N. America, West Indies, S. America (parts), Far

East, south eastern Asia. Habitat: Temperate and subtropical zone – forest type and steppe habitats (dioecious), in tropics – everywhere, from savannah to rain forest zone. Host range: Widely polyphagous species, in the tropics namely. Classification of parasite species-faunistic complexes: Far Eastern Deciduous Forest – *Ephedrus persicae*, *E. plagiator*, *Lysiphlebia japonica*, *Praon orientale*, Eurasian Steppes – *Lipolexis gracilis*, Nearctic Steppes – *Lysiphlebus testaceipes*. Selection of species to introduce: *Lipolexis gracilis*, *Lysiphlebia japonica*, *L. testaceipes*, probably also *Ephedrus* spp., *Praon orientale*. Unnatural host propagation: *Lysiphlebus ambiguus*, *Trioxys angelicae*, *Tr. aculephae*, *Praon abjectum*, *Pr. volucre*.

Myzus persicae. Its origin is unclear. Distribution: Cosmopolitan, except the northern areas. Habitat: Widely eurytopic. Temperate and subtropical zone – mostly in steppe habitats, penetrating in parks and orchards (dioecious), in tropics – everywhere. Host range: Widely polyphagous. Classification of species – faunistic complexes: European Deciduous Forest – *Praon volucre*, *Trioxys angelicae*, Far Eastern Deciduous Forest – *Aphidius gifuensis*, *Ephedrus persicae*, *E. plagiator*, *Lysiphlebia japonica*, *Praon orientale*, Eurasian Steppes – *Aphidius matricariae*, *A. picipes*, *Diaretella rapae*, *Lipolexis gracilis*, Nearctic Steppes – *Lysiphlebus testaceipes*, *Praon aguti*, *Pr. simulans*. Selection of species to introduce: *Aphidius gifuensis*, *A. matricariae*, *A. picipes*, *Diaretella rapae*, *Ephedrus persicae*, *Lipolexis gracilis*, *Lysiphlebia japonica*, etc. Unnatural host propagation: Various members of the Myzine groups of aphids are attacked by a number of aphidid parasites. Unnatural host propagation might be useful in some cases.

Toxoptera aurantii. A member of a smaller genus of the Aphidine aphids. Origin: South-east Asia. Distribution: Pan-tropical and subtropical species. Habitat: Forest type habitats (subtropical, tropical, etc.). Host range: A widely specialized species in the tropics, it follows the Citrus spread into the subtropics, where it attacks a certain number of other plants as *Thea*, *Camelia*, etc., nevertheless, in the northern areas it is more strictly specialized. Classification of parasite species-faunistic complexes: Far Eastern Deciduous Forest – *Ephedrus persicae*, European Deciduous Forest – *Lysiphlebus ambiguus*, *Trioxys angelicae*, Eurasian Steppes – *Lipolexis gracilis*, *Lysiphlebus fabarum*, Nearctic Steppes – *Lysiphlebus testaceipes*. Selection of species to introduce: *Ephedrus persicae*, *Lipolexis gracilis*, *Lysiphlebus ambiguus*, *L. testaceipes*, *Trioxys angelicae*. Unnatural host propagation recommendations: Parasites of the Aphidine aphids (*Trioxys aculephae*, etc.).

Toxoptera citricidus. Its origin is in tropical areas of south-east Asia. Distribution: Tropical belt of the world (America, Africa, Pacific Islands, Australia, Japan, China, etc.). Habitat: Primarily tropical rain forest, penetrating into cultivated habitats of similar character. Host range: It prefers Citrus species, but attacks also some other plants (the Rutaceae). Classification of species-faunistic complexes: Not known because of insufficient knowledge. Selection of species to introduce: Unknown due to lack of knowledge. Unnatural host propagation: Numerous parasites of the Aphidine group might be useful.

– *Coffee and cocoa*. (S. America and the West Indies) *Theobroma cacao*, a member of the family Sterculiaceae, is believed to be indigenous in tropical America, having originated north of the equator. It is distributed and grown today in many parts of the world, the most extensive cultivation being in West African countries.

Coffea arabica, a member of the family Rubiaceae, is apparently indigenous to tropical Africa. It is widely distributed and cultivated today, namely, in S. America, C. America, the West Indies, east Africa, south-east Asia, etc.

Both cocoa and coffee plants are the indigenous members of a tropical rain forest community, either of African or S. American type.

Two pest aphid species are generally mentioned as the pests: *Toxoptera aurantii* and *Aphis gossypii*, to a lesser degree *A. craccivora*, *A. spiraeicola* etc., may also be mentioned. Generally, the pest complex is almost identical with that of Citrus crops, so that no more detailed records on parasites are mentioned here (see above, Citrus). - *Alfalfa*. This and the following research project have been dealt with independently by American authors.

Therioaphis trifolii is an introduced pest into the U.S.A. Search for parasites was undertaken in the Old World districts, in the Mediterranean and its neighbourhood, to ascertain the composition of the parasites attacking the pest in its native country. The pest aphid is practically restricted to the steppe-semidesert areas of the Old World, so that it seems to be attacked by some specialized members of the Eurasian Steppes faunistic complex. The search was successful, three parasite species, two of them being aphidius, were found, introduced and successfully established in California. With respect to the work of Californian authors and valuable results obtained, it seems probable that parasite populations obtained from C. Asian deserts, which exhibit more severe conditions as to the cool winter namely, would apparently be also useful, they might occur in such districts in California where the Middle East parasite populations fail to establish.

Acyrtosiphon pisum, another introduced pest, is successfully controlled by an introduced Indian parasite, *Aphidius smithi*, in some areas of California, its establishment in some districts seems to be impossible due to extreme climatic conditions. In our opinion, the other parasites such as *A. ervi*, their populations from Europe and C. Asia, might be useful in covering the existing gaps in the present day biological control of the pest in California.

- *Walnut*. *Chromaphis juglandicola* is an introduced aphid, being found a pest in some areas of California, U.S.A. The American workers have introduced and successfully established the parasite *Trioxys pallidus* in California, the material being obtained in southern France. In our opinion, search for parasites of *Chr. juglandicola* in all European Deciduous Forest areas would be necessary to establish the full complex of parasites: at least *Praon flavinode*, co-existing with *Trioxys pallidus* in the mentioned zone as a parasite of various forest Callaphidid aphids, would be recommended to be introduced as well. Moreover, parasite populations from C. Asia might apparently exhibit valuable specific features as to the adaptation to extreme conditions of climate.

- **FURTHER RESEARCH.** We believe that one of the main tasks of the basic research on geographic distribution of parasites is to ascertain the composition of parasites in various parts of the world, the results being applied in elaborating the Biological control programs.

Both economically valuable and "indifferent" species, i.e. the parasite groups as a whole, must be dealt with, as only such research work may result in useful generalization and elaboration of rules for introduction work in biological control.

The research of faunistic complexes of parasites seems to be most helpful in the case of biological control of cosmopolitan and widely distributed species. In the case of specialized aphid pests, the classification may enable, at least, to give general characteristics of the species.

REFERENCES. Note: References on islands are not included. 8, 10, 17-8, 28, 35-6, 42, 78, 82-3, 84, 92, 93, 94, 96, 99, 100, 112, 116, 129, 134-42, 179, 191, 193, 203, 212, 213-4, 226, 230, 231, 232-3, 234, 251, 264, 269, 275, 276, 286, 287, 289, 292, 301, 307, 310-1, 313, 318, 320, 334, 395, 415, 436, 462, 465, 466, 475, 479, 495, 496, 509, 511, 531-4, 540-2, 550, 556, 557, 560, 566, 580-5, 593, 610, 614, 618, 622, 633, 634, 637,

661, 662, 667, 679, 682, 698, 703, 720, 723, 728, 737, 741, 745-6, 751, 758, 775, 779, 783, 793, 794, 796, 799, 809-14, 817-8, 819, 847-8, 858, 859, 872, 879, 880, 900, 912, 925, 931, 933, 936, 942, 949, 955, 956, 965, 975-9, 1004, 1006, 1008, 1017, 1047, 1049, 1057, 1069-70, 1078, 1081, 1082, 1087, 1104, 1117, 1125, 1129-30, 1134, 1137, 1179-82, 1187, 1191-2, 1221, 1223, 1235, 1243, 1249, 1261, 1266, 1282, 1309, 1325, 1327, 1330.

Foci in Nature

The classification of foci is one of the rather specialized topics of ecological research of the aphid parasites, we might really say one of the conclusive points of field ecology research. A good knowledge of taxonomy, bionomics, host specificity, distribution, dispersal, host-parasite relationship, community structure, etc., is essential before such research can be undertaken. Applied research work, connected either with indigenous or introduced species, must also start from classifying the existing or expected relations of a parasite species studied in the environment.

The classification and research of foci of aphid parasites is a new research trend, being dealt with by the author since about 1959, while incidental approach with no detailed and comprehensive classification can be found in papers of various authors (see below). The research of foci is a trend which is both highly required and stimulated by the applied research of today.

The occurrence of parasites in various environments has been an object of research by many workers. However, especially in the earlier years, no systematic study was undertaken, the problem being touched on mostly incidentally. It is just the recent period with an integrated control program which stresses the necessity of knowledge of the occurrence of natural enemies in the controlled areas. Therefore it seems to be useful to present in this book a brief review of opinions.

SPENCER (1926) listed in a scheme the interrelations of aphids, their parasites and hyperparasites on different crops, showing the interrelations of the fauna of different crops as well; non-cultivated lands, however, were not dealt with, the crops and non-cultivated lands being separated by this way.

Although dealing with *Encarsia*-parasite of *Oregma lanigera*, HAZELHOFF (1929) was apparently the first who recognized the significance of certain sources of aphid parasites in nature in connection with their dispersal to old and young fields of sugar cane in Java.

FLUKE (1929) has recognized, in connection with the research of natural enemies of *Acyrtosiphon pisum*, that a small field of peas near an open wood was practically free from aphids, the syrphid larvae and eggs being common. Another field, which was situated at a close distance but surrounded by cultivated land, pastures or bare fields, was exceedingly heavily attacked by aphids. His observations are rather valuable, although another situation would apparently occur with respect to parasites. Pea, an annual crop, would be inhabited by parasites only gradually via their dispersal from perennial field communities (alfalfa fields), there being no relation of these parasites to wood communities.

MARCOVITCH (1935) found the problem of maintaining a relatively high level of parasites and predators through the management of the environmental factors to be of basic importance, as without realizing it, the environment is constantly changed

by the farmer by crop rotation, planting data, etc. Thus, MARCOVITCH has recognized the difference and situation which exists in stable and unstable environments, as we call them today. In this connection, he made some experiments on the value of strip farming of various crops such as turnips, beans, peas, corn, cotton, cowpeas, okra, cucumbers and watermelons, in order to ascertain their significance as to the occurrence and dispersal of natural enemies of aphids, some plants being selected as more valuable than others owing to their attraction to insects through the supply of nectar or pollen or the presence of various host insects and their natural enemies. Naturally, there being no detailed records on the host range of separate parasite species, the relationship of these plants with respect to parasites was not dealt with except in a few cases.

PEAIRS (1947) has proposed a clean culture of crops and recommended the destruction of weeds and hedgerows surrounding the crop. This opinion seems to be rather isolated and perhaps not well documented by the detailed research of conditions occurring in field environments.

During the research of parasites of potato aphids in England DUNN (1949) nicely separated the experimental plots situated in a garden and in fields showing that an increased number of host plants for both potato and other aphids, found in the garden, resulted in a wider range of aphidophagous insects and produced artificial conditions not met with in the field. This author, therefore, has stressed the difference between communities with respect to plant diversity, as well as the significance of interrelations among various kinds of habitats.

TELENGA (1950) has mentioned the fact that aphids on annual crops are attacked by parasites mostly on the edges of fields, in the neighbourhood of uncultivated areas. This observation is undoubtedly valuable. Moreover, TELENGA dealt with the migration of aphids with respect to parasite foci. He believed that parasites of migratory aphids are sometimes capable of reaching mass numbers, however, their "reservoir" which could exhibit a certain influence in the following year does not originate. He also believed that this is due to the destruction of hibernating parasites in annual crops due to tillage in the autumn. TELENGA, too, expressed the opinion that the parasites die in late summer as a result of aphid emigration from the field. The latter conclusion disagrees with our observations and opinions and shows the ignoring of the basic differences between annual and perennial crops with respect to parasite occurrence and in general, not to speak of the seasonal history of aphids and parasites on annual and perennial crops.

FEDOTOVA & RJACHOVSKY (1954) recognized the differences between the degrees of parasitism of *Acyrtosiphon pisum* by *Aphidius ervi* on perennial (alfalfa) and annual crops (pea), being incidentally quite near to pointing out the difference between chromosomal and temporary foci.

Parasites of *Brevitryne brassicae* in England were dealt with by GEORGE (1957). He also made observations on the relation of the *Br. brassicae* parasites to other aphids attacking adjacent crops and vice versa. Although his observations were not based on the knowledge of host range of separate parasite species, his attention paid to the interrelations among the fauna of different fields is rather significant.

ELTON (1958) stressed the significance of hedgerows as a reservoir for enemies and parasites of insect and mite pests of crops.

SEDLAG (1959) when studying the dynamics of *Brevitryne brassicae* and its parasite *Dicretella rapae* in Germany, found that there is almost a complete isolation of the parasite and host in spring. The parasite disperses rather slowly from separate contact points (i.e. foci—author's note).

LUZHETSKI (1960) has recognized the character of the distribution of parasites in

of various authors.

Biocenosis is a complex of organisms inhabiting a certain habitat. A special type of biocenosis associated with field crops is called agrobiocenosis or agroecosystem.

Habitat is a place inhabited by a certain biocenosis.

Focus of an aphid parasite can be classified as a part of a biogeocenosis, characterized by more or less characteristic habitats and by the presence of biocenosis to which the parasite and its host aphid(s) belong.

The idea of parasite foci is not new. As we have already mentioned, various attempts can be found in the literature to give corresponding names or classification, the "reservoir" or "refugium" being most commonly used. It is necessary, therefore, to explain our classification proposed in 1964 as well as to mention the reasons why the terms used by the authors were not accepted.

Refugia. When classifying the trends in applied biological control, BEIRNE (1962) mentioned the intensification of biological control as one of the trends. "Refuges" were discussed as "reservoirs for natural enemies, where they can survive disruptions of nearby cultivated areas, where there are alternative hosts for those parasites that need them, where there are alternative foods on which polyphagous species can survive in the temporary absence or scarcity of pest species, and where hibernation sites, nesting sites, and other necessities for development exist. Thus the establishment of suitable refuges should enable natural enemies that are not host-specific to be utilized effectively in biological control attempts and thus may be biological control of pests on annual plants".

The term "refugium" seems to be mostly used and well defined in zoogeography, especially in connection with the survival of certain faunas in certain places in case of a general succession of the faunas due to climatic and other changes. There is no doubt that "refugium" means a place to which a species or a group of animals (plants) has retreated for various reasons. Nevertheless, such a classification does not seem to fit in many cases, which exist in cultivated lands. If there is a case of cultivation of a virgin steppe, some areas are usually left, where the original and typical fauna of the steppe occurs, although the neighbouring environments were drastically changed: in this case, perhaps, the term "refugium" would perhaps be applicable too; we can generally mention the fact that the cultivation of large areas of virgin lands seems to have a deep and mostly suppressive influence on the original fauna connected with the virgin lands. Nevertheless, most of the species of insects that occur in the fields might often survive in a field if it is not ploughed in the autumn and they can be found both in the fields and in the "refugia" throughout the season. The tillage suppresses or eradicates certain species in cultivated plots and thus limits their occurrence to the "refugia" only. In this case, however, the places of fallow land, roadsides, balks, etc., cannot be classified as refugia. Other species do really try to find the uncultivated areas as they represent suitable hibernation sites, etc. Here again, the species can occur in the cultivated land during the season, but search for a suitable hibernation site in the autumn. The latter does not seem to be a "refugium" either as the species may emigrate here also from the virgin land. Similarly, we know various cases of crop cultures, which exhibit relatively stable features so that parasites can be found perennially in such communities, there being no need to retreat to a "refugium". Alfalfa fields can be mentioned as a clear example. This feature is apparent in a strip cutting program, which significantly reduces the influence of cutting crops on parasite fauna and crop field equilibrium, being in general based on the perennality of the environment via modifications of agrotechnical activities; in seed alfalfa, where there is no cutting, we can compare the true character of such a community. According to our opinion, at least in many cases of crops, we

have developed certain habitats, mostly unnatural due to monoculture growing, which must be inhabited by the parasites every year via dispersal from habitats under less cultivation influences. Habitat dependence of parasites here also plays a significant role. For example, after clearing a forest and growing cereals on the very same place instead, there is no doubt that the parasite species were gradually forced to retreat and occur in the neighbouring forest or in its remainders in the neighbourhood. But what has changed? Our observations on the habitat dependence of parasites have shown the strong influence of separate types of habitats. This means that the true forest fauna has no relation to the steppe (cereal field) fauna except in case of obligatory host alternating aphid species, where parasitization by different parasite complexes in forest and steppe does not represent a result of man's action but a result of a general evolutionary trend connected with the occurrence of a drier climate (forest - steppe). The forest "refugium", therefore, has generally no connection with the new fauna which inhabits the given plot. In cultivating a virgin steppe, of course, another situation would develop, as both the virgin and cultivated steppe are habitats of the same type, i.e. of "steppe" type.

The term "refugium", too, seems to bear a passive meaning, as if the parasites were forced to occur in such places. Nevertheless, various observations carried out on e.g. cultivation of virgin semidesert have shown that many original semidesert insects actively attack the crop grown on newly cultivated land, often being followed by the parasites, and many of them have become serious pests just for the simple reason that the carefully irrigated and grown plants represent a better food source for them. This means, to put it briefly, that we have not forced the insects—both the pests and their parasites—to retreat to refugia due to cultivation of new lands. Dispersal is a typical feature of every species. It would be better to say, therefore, that the question is more that of stable and unstable environments (see below).

Concluding, we should prefer to leave the term "refugium" for zoogeographical purposes.

Our classification of foci is more general, covering the whole classification of the occurrence and sources of parasites in nature irrespective of whether the parasite species are economically valuable or indifferent. Various kinds of communities have been classified in this connection, showing the various importance of such foci in a more or less cultivated landscape as well as in "virgin" land (see below). Therefore, while refugia seem to be restricted to cover a case of the sources of parasites (natural enemies) in nearly fully cultivated areas, the foci cover a much wider scope, including both the cultivated and virgin environments, classifying them with respect to the character of the community, peculiarities of host biology, etc. As we have shown, foci (clitonic) can be found in fully cultivated areas such as alfalfa fields as well, which does not seem to be true in the case of "refugia".

Reservoirs. Reservoirs may be understood as a synonym of refugia mentioned above. They are mostly classified as something more or less stable, of a permanent character, from where the parasites can disperse to neighbouring habitats (see: MACKAULA, in MACKAUER & STARÝ, 1967). They are, therefore, more identical with a part of the chronic foci of parasites as defined by the author. Otherwise, the same may be said of the reservoirs as of the refugia.

The research of foci of aphid parasites can be classified as a higher degree of faunistic research, being its necessary part, which is a basis to applied studies on natural limitation and aphid control. Naturally, a good level of taxonomic research as well as a perfect knowledge of the taxonomy of the group are prerequisites for such a type of work. A good knowledge of aphid biology, and praxis in field work is a further necessary point of this research work. This all clearly shows that the exhaustive

research of foci in a given country is a long-term matter; the terms of this research can be considerably shortened, however, when the whole problem is correctly understood and the research program is carefully planned. On such a base, at least a number of various habitats need not be dealt with, due to our knowledge of the host range of separate species, which exhibit similar features in related territories, such as European countries. Nevertheless, it must be kept in mind that the host range, both as to the habitat and host preference, can exhibit various geographically dependent peculiarities. For this reason, we have decided to deal gradually with the separate problems of this kind of research, the methods of research later being summarized in a schematical way.

TYPIFICATION. The undermentioned division of the foci is necessary for their rational typification to show the peculiarities in some relations of abiotic, biotic, geographical, and of other characters, as well as their origin in relation to the activity of man. Various criteria are used according to which the foci are divided:

~ *Number of parasite species.* A. Monospecific focus. It includes only a single parasite species, or one parasite species of a given host aphid.

Example: *Acyrtosiphon pisum* in an alfalfa field can be attacked by *Aphidius ervi*. The alfalfa field therefore, represents a parasite monospecific focus with respect to the aphid.

Truly monospecific foci, i.e. such foci where only just a single parasite species is generally present, are rare, as there are mostly several species of parasites present, although they may not have any interrelations due to their different host range.

B. Bi- and polyspecific focus. It includes two or more parasite species of a given host aphid, or more parasite species of different aphid species.

Example: *Aphis fabae*, occurring in forest-type habitats such as edges of woods, groves, orchards, etc. in C. Europe is attacked by three parasite species, *Ephedrus plagiator*, *Praon abjectum*, *Trioxys angelicae*. These habitats represent polyspecific foci of parasites.

~ *Total length of existence.* A. Old focus. They are present in stable environments with relatively stable communities.

Example: Forest, virgin steppe, etc.

B. Recent focus. They are present in various environments, which have mostly originated in connection with the activity of man.

Example: Ruderal communities, with a rich weed flora and corresponding fauna of aphids and parasites.

Example: Cultivated areas (fields).

~ *Character of origin.* A. Autochthonous focus. Principally, we have to include in this group only such foci which have developed in nature independently of man's activity; strictly speaking only foci occurring in virgin land areas would be included here:

Example: Virgin desert, virgin steppe, forests, etc., and foci occurring in these habitats.

However, today it is sometimes difficult to separate this kind of foci as they often became mixed with the newly formed types of cultivated areas. Nevertheless, their research is of basic importance wherever possible as they represent the foundation-stone of all the classification of the foci.

B. Anthropurgic focus. These foci have originated as direct or indirect results of man's activity.

Example: All the cultivated landscape includes such foci: fields, orchards, pathways, roadsides, fallow land, ruderals, etc.

Example: Colonization of parasites in biological control program can be included here as well (confined release, etc.).

However, this group of foci cannot be strictly divided or classified either. As we have mentioned in various chapters, the cultivated landscape is undoubtedly rather original in many respects, its fauna—though having a characteristic composition as well—has originated from the sources of original virgin landscape. The research of the fauna of virgin and cultivated steppes carried out in the U.S.S.R. represents a clear demonstration.

— *Length of seasonal existence.* A. *Temporary focus.* The character of such foci with respect to their existence during one year is seasonal. They occur for a longer or shorter period of the season.

Example: Groups of *Cirsium*-plants (weeds) infested by *Aphis fabae* in cereal fields. The aphid is later parasitized by *Lysiphlebus fabarum*, which moves from there after the emigration of aphids.

We presume it is necessary to stress the temporary character of these foci. Many authors are under the impression that the absence of parasites e.g. in cereal fields is due to the tillage in the autumn, etc., however, this does not seem to be a justified opinion as the parasites leave the field searching for other aphids in the related environments such as fallow lands, etc., being therefore absent in cereal fields long before the fields are ploughed.

B. *Chronic focus.* The chronic foci represent sources of parasites during the whole time of their existence. Naturally, this type of foci is influenced seasonally as well (population densities, etc.). The stable character of this type of foci is most important.

Example: Waste places in the neighbourhood of potato fields or rape fields (C. Europe) are covered with weeds, e.g. *Atriplex*, *Chenopodium*, etc., the weeds mentioned are infested in addition to other aphids, by *Hayhurstia atriplicis*, which is one of the hosts of *Diaeretiella rapae*, and the parasite can be found in such places throughout the whole season. The parasite, simultaneously, moves from there to potatoes and sugar beet fields, where it infests the pest aphid *Myzus persicae*, or to rape fields, where it attacks *Brevicoryne brassicae*.

Example: Alfalfa field (C. Europe). It is a perennial community, where *Acyrtosiphon pisum* and its parasite *Aphidius ervi* can be found throughout the year. Both aphid and parasite overwinter in the field as well, and they both disperse from here to leguminous annual crop fields (pea), where their foci are only temporary (annual character—unstable environment).

It must be added that a parasite species may be present in a chronic focus also in a quiescent state during a certain part of the season; then we have to classify the focus as a chronic one as well, although it might seem that it is temporary, due to the temporary occurrence of parasite adults. Hibernation sites as well as various places where diapause cocoons of parasites are found can be mentioned as examples.

— *Specific composition of parasites.* This criterion is of basic significance as on this basis, we have to decide whether a parasite focus is useful economically or not.

A. *Indifferent focus.* Such foci contain parasites of economically indifferent aphids, which do not include any economically important aphid species within the range of host specificity.

Example: Waste places or ruderals covered with *Achillea* sp., *Artemisia* sp., or *Tanacetum* sp. These plants have a rather specialized fauna of aphids and parasites, which is entirely indifferent to agricultural crops in the neighbourhood.

B. *Useful focus.* Useful foci include parasites of pest aphids.

Example: Field boundaries covered with *Salvia* sp. (C. Europe) plants are infested by *Aphis salviae*, *Plantago* spp. by *Aphis plantaginis*, etc.; these aphids are also hosts of

Lysiphlebus fabarum, *Lipolexis gracilis*, which parasitizes also quite a number of pest aphids (e.g. *Aphis fabae*, *A. tracicivora*, *Brachycaudus cardui*), that occur either in the area of the given focus or in the neighbouring cultivated areas.

Example: *Arundo donax* reeds (S. Europe) are commonly attacked by *Longicuneus donaris*. The aphid is economically indifferent, but its parasite—*Aphidius transcaspicus*—is an effective parasite of *Hyalopterus pruni* that can be found either on Phragmites-reeds or on orchard fruit trees (peach) in the neighbourhood.

C. Noxious focus. The classification of aphid parasite foci as noxious is a subjective matter. Some aphids are important producers of honey-dew. From this viewpoint, their parasites could be—and their foci as well—considered as undesirable.

RESEARCH. One of the principles of understanding the problems connected with the research of foci is to keep them as a part of the biogeocenosis or ecosystem. Although we separate the foci because of methodic reasons in a certain way, the basic connection is of primary importance. Parasites are only a part of the food chain connected with a certain aphid species. There are also other natural enemies as members of the food chain mentioned, there being various and changeable relations between the members of this food chain in the course of the season with respect to changing environmental conditions. A given biocenosis has a certain structure, there are also other food chains and they may exhibit various relations to the given food chain.

Parasites are a small group of the whole biocenosis, so that the knowledge of their relation to the place of the biocenosis's occurrence, i.e. to the habitat, is necessary. Various kinds of habitats exhibit various features and their basic knowledge at least is necessary for the classification of foci. Different conditions occur in a forest, in a virgin steppe, in a cultivated steppe, in trees and in undergrowth, in new and old orchards, in dry and irrigated land, in annual and perennial crops, etc.

Fauna of parasites is basically associated with various floristic zones. The same is true of the foci. This means that foci must be principally related to a certain type of floristic community. Further, if necessary, they can be related to separate microhabitats as well.

There is no doubt that our classification and the entire foci research is based on field observations and their evaluation. For this reason, it would be necessary to practically prove whether our presumptions based on field studies are really true and correct. We could collect identical parasites from different aphids, however, there may be certain biological races or strains and the presumptions as to the significance of foci would be thrown into doubt. Literary records, such as those of GEORGE (1957) and SEDLAG (1959) and our own observations on *Myzus persicae* parasites (*Diaeretiella rapae*) show really different situations occurring in different countries, though closely related geographically. It was ascertained that *Diaeretiella rapae*, the main parasite of *Brevicoryne brassicae*, does not attack *Myzus persicae* in England, although it did so in the laboratory (GEORGE, 1957). Moreover, SEDLAG (1959) has shown that both *Myzus persicae* and *Brevicoryne brassicae* are attacked by the parasite in Germany. We can only confirm the observations of SEDLAG giving in addition the fact that besides the two aphids mentioned it is also *Hayhurstia atriplicis*, a common aphid occurring on *Chenopodium* weed, which is attacked by the parasite. This fact might indicate that we must be careful in generalizing and especially in the application of results obtained in one country to conditions of another country. Geographical variation in host preference is a well known fact.

We have made a number of tests transferring parasites from one host to another in the laboratory to show whether the presumed field relations can be obtained also in the laboratory; at least a few of the cases dealt with should be mentioned:

Aphidius ervi. It is a common parasite of *Acyrtosiphon pisum* in C. Europe. Faunistic research has shown that the species also attacks *A. spartii* on *Sarothamnus scoparius*, and *Microlophium evansi* on *Urtica dioica*. As both *Sarothamnus* and *Urtica* growths represent perhaps important foci of the parasite, we tried to prove this through laboratory tests using *Acyrtosiphon pisum* as host. All the tests were positive, the parasite attacked and completed its development on the above mentioned hosts in the laboratory. These laboratory results supported our original assumption based on field observations that *Aphidius ervi* attacks all three species of aphids as well as the significance of its foci in nature.

Praon abjectum, *Trioxys angelicae*, *Ephedrus plagiator*, *Lysiphlebus fabarum*, *L. ambiguus*. All these species, being mainly parasites of the Aphidine aphids, were tested in the laboratory on the basis of identical principles in a similar way. Also in these cases the laboratory tests verified the field observations.

Generally, we can only stress the necessity of careful and sufficient extensive field observations and additional laboratory tests on the host specificity of separate parasite species especially in cases of somewhat different geographical areas. Many samples taken at various localities will bring at least general data on microhabitat preference of separate species as well.

Interspecific relations existing in a focus are determined by the structure of the given ecosystem. In this connection, there may be species occurring independently of each other in connection with their host range, or—if being parasites of the same aphid species—they may stay in cooperation, competition, etc. among themselves or with other members of the corresponding food chain such as predators or aphid parasites of other groups.

STABILITY OF ENVIRONMENT

— *Natural ecosystems* may be classified as ecosystems that developed in nature during the process of evolution irrespective of the influence of man. Today, the truly natural ecosystems seem to be comparatively rare. According to SCHMITHUSEN (1961) extensive natural landscapes can be found only in districts where the conditions of environment are not useful or suitable for colonization and civilization by man: Ice and dry deserts, high mountain districts, separate districts of tropical and mountain forests, and partially also boreal forests and tundras. All the other territories of the earth, the grassy districts in the tropics namely, are changed to a high degree by the activity of man. In many cases, we can hardly distinguish between the natural and cultivated landscape.

Parasite foci in natural environments are generally characterized by a more stable character, although they can be both chronic and temporary.

— *Cultivated ecosystems or agrobiocenoses*. Specific features of ecosystems that developed under the influence of human agriculture were recognized by a number of authors. BEY-BIENKO (1962) recognized that the plant cover of an agrobiocenosis differs basically from the plant cover of primary cenoses by a number of characters:

1. There is only a restricted number of plants in an agrobiocenose, from which a single species represented by the cultivated crop (or there are several species in mixed crops) is the cenotic dominant and constant, the other plants being weeds and they ideally should be eliminated or absent.

2. The resistance of plant cover in an agrobiocenose is only due to the agricultural activity of man. The regular reaping of the biological production (harvest) is substituted by corresponding agrotechnics.

3. The replacement of the agrobiocenose is also under man's influence due to a crop rotation system.

Nevertheless, besides these peculiarities, the agrobiocenose is characterized by the basic feature of biocenoses, i.e. resistance of plant cover composition. This is true of the fauna as well.

UVAROV (1964) summarized the problematics connected with the disturbance of the environment due to human agriculture with respect to developing countries namely, the main types of land development affecting insect populations being: deforestation, afforestation, forest shelter-belts, utilization of natural pastures, irrigation, and amelioration.

SMITH & REYNOLDS (1966) classified the agrobiocenoses under a special term "agroecosystems", which is identical with agrobiocenoses, keeping this system as man-produced, or rather man-modified.

Cultivated landscape includes simultaneously a certain amount of non-cultivated land that is represented by fallow land, roadsides, waste places, etc. Non-cultivated lands are generally known to exhibit greater diversity of plant cover and a corresponding greater diversity of fauna also when compared with the almost pure stands (or mixed stands) of cultivated crops. Non-cultivated land, therefore, generally represents more stable environments than cultivated land. With respect to parasite foci, this statement is rather important as the non-cultivated land includes various foci of parasites which disperse from here to the cultivated neighbourhood. These parasite foci, therefore, seem to be very important in the cultivated landscape.

The perennial character of an ecosystem does not mean at the same time that the ecosystem is stable with respect to aphids and parasites, although a stable character is mostly to be expected in perennial environments. The peculiarities of the aphid life-cycle and parasite biology seem to play the main role. As is known, certain plants may or may not be useful food for aphids throughout the season. Thus the aphids may or may not be present in such perennial communities throughout the whole year. Requirements of different species play also a role so that one and the same perennial crop may represent a continuous source of food for some aphids, while being only a temporary host of other species.

Example: Alfalfa field (C. Europe). *Acyrtosiphon pisum* as well as *Therioaphis trifolii* are perennial inhabitants of alfalfa fields, they occur here throughout the whole season and hibernate in the egg stage. *Aphis craccivora*, on the contrary, hibernates as an egg on alfalfa, but it emigrates from there for a certain part of the season. An alfalfa field, with respect to *Acyrtosiphon pisum* and *Therioaphis trifolii* can be classified as a habitat containing chronic foci of parasites, but as to the parasites of *Aphis craccivora*, there are only temporary foci, the environment being unstable due to a seasonal lack of the host.

Example: Apple orchard (C. Europe). For parasites of *Dysaphis* species this habitat may include chronic foci. *Ephedrus persicae* enters the diapause before migration of its *Dysaphis* hosts, and occurs in a diapause state till the next season; although partially in a quiescent state, the parasites are present perennially in the habitat. Another species, *Ephedrus plagiator*, does not enter the diapause and after the migration of the *Dysaphis* species it attacks other host aphids in the orchard. In this case too, an orchard may represent a habitat including chronic foci of the parasites of *Dysaphis* species. *Aphis pomi*, a monoecious aphid, and its parasite (*Trioxys angelicae*) represent a similar case as to the perennial occurrence of parasites. Naturally, the composition of the fruit trees in the orchard is important as to the presence of various alternative hosts of the parasites mentioned.

Example: Citrus orchard (Cuba). In monoculture Citrus orchards the aphids are seasonal pests, attacking Citrus only when it is in vegetative growth, they do not attack it when it is in a quiescent state (*Toxoptera aurantii*, *Aphis spiraeicola*). If no

other host aphids are present in the orchard (undergrowth), the parasites (*Lysiphlebus testaceipes*) would be unable to survive the long absence of their hosts and they would have to search for other hosts in the neighbourhood. The undergrowth—the possible source of alternative hosts—may determine the character of foci in Citrus orchards. In some cases, when there is no undergrowth (clean cultivation system), the chronic foci of parasites may be present in the close orchard neighbourhood (shrubs, ornamentals, road-side trees).

Sugar beet field (C. Europe). Sugar beet grown for sugar production is an annual crop, grown for seed it is a biennial. The seed sugar-beet is therefore a relatively stable environment, occurring for two seasons at the same plot. It might seem to be a case identical to that of alfalfa, but it is not. *Aphis fabae*, occurring on sugar beet during the season, is a dioecious species, present only seasonally on the crop, whether it is an annual or biennial crop. This feature of aphid biology makes the environment to be of unstable character, although it is a biennial crop.

If the peculiarities in aphid biology are omitted, there is no doubt that there are differences between the annual and perennial crops as to their general features. However, as it is apparent from the gradual dispersal of the fauna to newly seed perennial crops, the first year's perennial crops and the annual crops are rather similar throughout the first season, the differences being seen, however, before and at the end of the season, due both to the character of the plant and crop rotation system (tillage and general change of ecnose in the case of annual crops, no tillage and stable character of perennial crops).

—FACTORS. The basic factor influencing the stability of environment is the structure of a given biocenosis. This structure is the result of a long evolution, resulting in a relative equilibrium. Some of the biocenoses, results of a long evolutionary process, are of rather solid structure and of great stability under natural conditions. Others are of a less solid structure owing to various reasons: they may be evolutionarily younger, they may change due to a change of climate, etc. As is known, a solid structure of a given biocenosis is mainly dependent on the diversity of species—the more diverse they are, the more stable the community is. As is apparent, the character of parasite foci is determined by the general character of the community to which they belong as its part. Chronic foci are typical just for the stable environments, while temporary foci may be a feature of a less stable character of the community at least with respect to aphids and their parasites.

Man's agricultural activities are practically concentrated in growing monoculture of certain plants, the crops. The trend towards monocultures greatly simplifies community structure (BURNETT, 1961). This results, on the one hand, in outbreaks of certain insect species, on the other hand, a community with a smaller diversity of species can be more easily invaded by a new member such as an introduced pest. The significance of species diversity for the relations in Brassica crop mixed and pure stands was shown by FIMENTEL (1961). Therefore, we can generally summarize the situation in that the growing of monoculture by man (i.e. the origin of agrobiocenoses) resulted in a simplified structure and corresponding results. Moreover, and this is the next important feature, besides growing monoculture, man has developed certain agricultural practices in trying to grow the crops more easily and successfully. A cultivation system, crop rotation system, cutting system, harvesting system etc., and insecticidal treatments appeared. It is a question of to-day to evaluate such practices with respect to ecosystems in connection with an integrated control program. It was well recognized by Californian authors (see integrated control chapter) that agricultural and control practices which reduce the diversity of species may be working in exactly the wrong direction, as it is a typical feature of a healthy

diverse biotic community not to be easily invaded by exotic forms and to exhibit considerable activity to adjust the invaders (v. d. BOSCH, 1965). In connection with this ascertainment, special programs such as a strip-cutting program, strip farming program, development of uncultivated land to conserve natural enemies, etc., were developed with the main task to make the crop community as stable as possible. These programs can be classified as making up for the mistakes made by agricultural practices with respect to the ecosystems.

As already mentioned, the parasite foci exhibit peculiar features with respect to their occurrence in various kinds of crops. While chronic foci of parasites may be present in certain crops, e.g. alfalfa and other perennials, and may be conserved through various practices as well, this is not the case of parasite foci in annual crops as just their temporary character does not permit the continuous occurrence of aphids and parasites on one plot throughout the whole year. The significance of neighbouring land comes into scope. In the neighbourhood of annual crops there exist various plots in which both pest species and their parasites may be found. The dispersal of aphids to monocultures of annual crops means practically their occurrence without parasites there at first and outbreak numbers may be reached: immigration of aphids may influence the stability of the agrobiocenose, while this is not the case of diverse natural ecosystems in which parasite foci are present.

~ **APHID MIGRATION.** Communities may be stable, but aphid migration can make them unstable with respect to aphid parasites. There are several cases to be distinguished:

A. There are several aphids, both obligatorily and facultatively host alternating, present in a stable environment as well as parasites, which are widely specialized. Obligatory migration of an aphid species from such an environment does not apparently cause any deep changes in the stability of the system, as the parasites are able to parasitize other aphids present. The same is true of the immigration of an aphid to this system, the parasites again covering the aphid.

Example: Deciduous forests of C. Europe, with *Ephedrus plagiator*, *Praon volucre*, *Trioxys angelicae* and other parasites present.

B. There are only monoecious aphid species present in an environment, so that only facultative host alternation occurs. Parasite species are also present continuously, close connection between host and parasite apparently appearing in consequence. No changes in community stability due to aphid migration can be observed.

Example: Deciduous forests in C. Europe, Callaphidid aphids and their parasites.

C. Aphid species present is a dioecious one (obligatory host alternation) being therefore present for a part of the season only. This can influence the stability of the environment due to peculiarities in parasite biology in different ways:

(a). Parasites exhibit obligatory quiescent states in which they survive the period of host absence, they remain in the same ecosystem for the whole season. Aphid migration does not cause any significant changes in ecosystem stability.

Example: Deciduous forests in C. Europe. *Dysaphis* species and their parasites (*Ephedrus persicae*).

(b) Parasites do not exhibit obligatory quiescent states, they are unable to survive the period of host absence and disperse therefore to the neighbouring environments. In such a case, the stability of the ecosystem is changed as there will be no parasites present the next year, due to the seasonal lack of aphids and lack of corresponding parasite adaptation.

Example: *Phragmites communis* in C. Europe. *Hyalopterus pruni* immigrates to reeds in late spring and emigrates in the late autumn, the ecosystem being, however, a stable one—a natural perennial community. The composition of species is relatively

poor due to practically natural monoculture existence, so that no alternative hosts are found by parasites on reeds when *H. pruni* is absent.

D. There are several aphid species present in the ecosystem, the parasites being strictly specialized (in the framework of the given ecosystem).

Example: Alfalfa - *Acyrtosiphon pisum*, *Therioaphis trifolii*, in C. Europe.

In this case, the influence of the facultative host alternation by aphids is of the same type as in case B.

We summarize the state of aphid migration and stability of environment in such a way that facultative host alternation does not usually influence the stability of an environment as the aphids continue to occur in this environment, although infesting other host specimens. Obligatory host alternation by aphids, on the contrary, may influence environmental stability in case there are no alternative hosts present in the community and the parasites are not adapted to the host aphid life cycle by entering quiescent states.

Aphid migration and its seasonal occurrence make the unstable environment even more unstable or relatively stable during certain parts of the season.

Example: In certain annual crops, such as sugar beet, the aphids are present for a relatively short period, while in others the aphid—although a seasonal inhabitant as well—may be present for a greater part of the season.

Unstable environments mean less possibility of aphid parasitization due to the unstable character of parasite presence in a given area. For this reason, immigration of an aphid into an unstable environment in crop fields especially supports the probability of outbreaks of aphids due to the lack or low population level of parasites in the initial stage of aphid appearance.

Ecosystem stability with respect to aphid migration is also geographically variable, which is due to geographical peculiarities of the aphid life-cycle. As an example, two species of reeds may be mentioned:

Arundo donax. In S. Europe it is perennially attacked by the aphid *Longumiguis douaisi*. This aphid is parasitized by several aphid parasites, by *Aphidius transcaspicus* namely, which occurs here throughout the whole season, exhibiting seasonal fluctuations in density. There may be a difference between the seasonal history in relatively colder regions—in S. Europe (French Riviera)—the aphid and parasite hibernate due to a somewhat colder winter, while they occur apparently perennially in warmer regions (Asia Minor, etc.). It must be stressed that the aphid is a monoecious species in all its distribution area, so that no changes in host alternation with respect to different areas of distribution can be found.

Phragmites communis. This species of reed is found in both C. and S. Europe, in Asia Minor, etc. The character of the community is stable, but in the north there is a period of vegetation hibernation, this not being the case of the southern districts, where *Phragmites* is an evergreen plant. This feature has its effects on *Hyalopterus pruni* as well. In the north, in C. Europe and further north, the aphid is a typically dioecious species, alternating *Prunus* and *Phragmites* as hosts. In southern Europe, in its colder parts, there is still host alternation and hibernation of the aphid, while in Asia Minor, besides obligatory host alternation, parthenogenetic populations are known to occur perennially on *Phragmites*. Therefore, in C. Europe the *Phragmites* growths are an unstable ecosystem with respect to the occurrence of parasites of *H. pruni* due to the aphid life-cycle, while ecosystems associated with the same plant are mostly stable due to the partially perennial presence of the aphid in warmer parts of its distribution area, such as Asia Minor.

—JOCT OF PARASITES. There seems to be a general rule that chronic foci of parasites are connected with stable environments, peculiarities of aphid biology being positive

as well, while temporary foci of parasites may be found both in stable and unstable environments.

— **HOST SPECIFICITY.** It seems that restricted host range mostly means the occurrence of a parasite species in stable environments exclusively; such a feature might well be understood because of host parasite coincidence that is just rather close in case of a strictly specialized parasite.

Wider host range, on the contrary, enables the given parasite species to occur both in stable and unstable environments. Aphid host life cycle, host range of the given parasite species, and the neighbouring environments play the most important role. Wider host range may support the character of the community to be more stable in the case that more aphid hosts falling within the range of parasite are present in this community.

— **NUMBER OF SPECIES.** Generally the greater number of parasite species supports the species diversity and thus the stability of an ecosystem. However, it is necessary to add that the host specificity of the separate parasite species is significant, besides the number of the species present. The number of parasite species must be related to a given aphid species to show the true role of parasites in the ecosystem stability: if there are more parasite species of an aphid present, the ecosystem is usually more stable due to the cooperative action of parasites that replace each other in action. *Aphis fabae* and its three parasites (*Ephedrus plagiator*, *Trioxys angelicae* and *Praon abjectum*) in deciduous forests in C. Europe may be mentioned as an example. Contrary to this state, there may exist several parasites in a community, each of them being, however, a strictly specialized parasite of one aphid species with no connections among themselves in consequence, community stability is lower as there is no chance of parasite cooperation and replacement. Example: Alfalfa field and complex of aphids and parasites in C. Europe (see above).

— **CONSERVATION.** All the activities directed towards the conservation of the stability of environments may be classified simultaneously as useful for the conservation of parasite foci. Strip cutting and strip farming programs are the clearest examples. Both these kinds of manipulating the environment with respect to parasite occurrence are connected with monoecious aphids and their parasites, which perhaps are better objects for such an activity. In dioecious aphids, however, a peculiar situation may develop, as these aphids emigrate in a certain part of the season from a given habitat, immigrate to another one, leave it later as well and re-immigrate to the original habitat again. As we have shown earlier, the adaptation of parasites to such a cycle of their hosts is either in wider host range or in development of quiescent states. Wider host range comes into action in natural conditions, i.e. in diverse and stable communities, while in cultivated environments there can be a lack of alternative hosts for various reasons, of which the influence of growing monocultures seems to be the most important one.

In such cases it is usually recommended to develop higher diversity in plant cover, e.g. in an orchard through the planting of hedgerows on edges, non-cultivation of undergrowth, etc. Nevertheless, this is not always possible, especially in the case of introduced parasites that, although being more widely specialized in their native country, do not find alternative hosts in the release area and are therefore practically "monophagous" here. However, it appears a problem now as to the coincidence of parasite and host-aphid life cycle in the release area if the aphid is a dioecious species. In such a case, we should try to develop small plantings of host aphid secondary plants in an orchard to enable the aphid to occur there perennially, although its population is low during a certain part of the season, and to manipulate the environment in such a way as to develop a more stable ecosystem with respect to the newly

introduced parasite. An example for illustration: *Hyalopterus pruni* is a dioecious aphid in C. Europe, alternating *Prunus* sp. and *Phragmites communis* as its host plants. In southern Europe and Asia Minor the life cycle is similar except that there can also be found some continuously parthenogenetic populations occurring perennially on *Phragmites* exclusively. In southern districts, the aphid is attacked, besides others, by *Aphidius transcaspicus*, which is also a parasite of *Longicuneus donacis* on *Arundo donax* reed, which is a monoecious aphid. Therefore in the case of *Arundo donax* reed being present in the orchard or its neighbourhood, the parasite may occur perennially as a parasite of *Longicuneus donacis* and may survive the temporary absence of *Hyalopterus pruni* on *Prunus* trees. In this way, due to the diversity of plant cover, the orchard is a relatively stable environment with respect to the given parasite. In this case, *Phragmites* reeds, as a source of *H. pruni* pest, were also found to be undesirable in orchard environments or in the neighbourhood just due to the *Arundo donax*. However, another situation appeared when *Aphidius transcaspicus* was introduced into C. Europe as *Longicuneus donacis* is absent there, the parasites host range being therefore restricted to a single host species i.e. *Hyalopterus pruni*. In our experimental program we found in certain areas both *Prunus* orchards and *Phragmites* reeds to be in close proximity to each other, so that we can anticipate the parasite will be able to find its host in both the environments and develop the coincidence with the controlled host aphid. However, there are other orchards from which *Phragmites* reeds are rather distant. It is known that aphids usually exhibit greater dispersal power than the parasites so that we can expect that the parasite will hardly be able to disperse in a similar way. For this reason, we have planted some reeds in cages and placed them under the *Prunus* trees in an experimental orchard where *Aphidius transcaspicus* was released and attacked the aphid on *Prunus*. The aphid was really found later to occur on reeds as well as the parasite. Such a manipulation of the environment enabled parasite survival during a part of the season when the aphid would otherwise be absent.

DISTRIBUTION OF PARASITES. Foci of parasites represent certain patterns in parasite distribution and for this reason they exhibit the same features.

Geographic distribution i.e. distribution of parasite on a large scale, is dependent on their attachment to certain floristic zones. In these zones, too, parasite foci can generally be found.

Habitat distribution is rather important as to the foci of parasites. Separate types of habitats and associated communities determine basically the character of foci. It is well apparent how different are the foci in fields of various crops, non-cultivated land, etc.

Microhabitat distribution is also of great importance. Various species of parasites, although theoretically capable of occurring in certain habitats, are further differentiated with respect to microclimate differences. This feature is naturally seen both in the specific composition and significance of parasite foci in various habitats.

Geographic variability of the foci. Consequently, due to the geographic variability of habitat dependence, and host specificity of parasites, foci exhibit geographic variation. This feature of foci becomes apparent when the occurrence of the same parasite species in northern and southern districts of their distribution area is compared.

SEASONAL SUCCESSION. Ecosystems are dynamic associations, they exhibit seasonal changes due to responses of their members to conditions imposed by separate yearly seasons. These changes are regulated by the equilibrium of these separate systems,

which is determined by their structure. For this reason, seasonal succession may be recognized both in stable and unstable environments, although it may show various peculiarities depending on the community stability.

Aphids are a typical group which is often deeply influenced by the seasons. Production of various forms, migration, etc., all these peculiarities in aphid biology are directly or indirectly influenced by separate yearly seasons. In this respect, we can distinguish various aspects in the development of a given ecosystem in the course of the year. Two points of view on seasonal succession of aphids and their parasites in an ecosystem can principally be recognized:

1. Successive occurrence of separate aphid species. In many ecosystems several species of aphids occur, which appear successively in the course of the season due to their specific requirements. For example, in C. Europe, we can observe that in spring first the various *Dysaphis* species occur, followed by *Aphis pomi* in apple orchards; or in alfalfa fields, we can observe *Acyrtosiphon pisum* early in the season and only later *Therioaphis trifolii*. Such a seasonal succession of aphid occurrence may or may not be important for the parasites, the host range having the leading role in this respect; in case that a parasite attacks several aphids that appear successively in an ecosystem, it can occur there perennially with no peculiar adaptation to the host aphid biologies except the wider host range (example: aphids and their parasites on *Prunus domestica* in C. Europe); in the case that it attacks only one species, having no relation to others, whether they appear successively or not, it must be much more specialized to the host's seasonal occurrence (example: alfalfa aphids and their parasites in C. Europe). Such feature of foci succession are also important to the relation of species in the foci.

END OF THE FOCI. The foci of parasites in a given area or plot may cease to exist for various reasons. Their possibly chronic character is naturally relative in time and space. Here, we deal only with either the immediate changes of the environment due mostly to man's activity, or by gradual natural processes such as plant succession, while the natural temporary character of certain foci, host and parasite seasonal coincidence and corresponding adaptation, etc., are omitted.

Non-selective complex treatment, or incorrectly timed treatment may result in elimination both of the host aphid and its parasite in a given plot, or pest aphids may be eliminated while parasites can survive inside mummified aphids, although after their emergence, they cannot find any living aphids, or, a certain number of pest aphids may survive the treatment, while the parasites are eliminated. All these possibilities illustrate the deep influence of similar activities of man on parasite foci. Similarly, tillage, cutting, plant removal, all that can also result in the elimination of parasite foci in a given plot.

Of the natural factors, which may cause the end of the foci in a given plot, plant succession, causing deep changes in plant cover, seems to be the most significant. The occurrence of other plants means the presence of other aphids, changes of microclimate, etc., resulting in basic structural changes in the community and naturally in the parasite foci too.

HIBERNATION AND AESTIVATION. Quiescent states in parasites have developed as an adaptation to unfavourable conditions of the environment, caused either directly by the influence of climatic conditions, or by the peculiarities in the aphid life cycle.

In aphid parasites, quiescent state periods are spent in the stage of the last instar larva inside mummified aphids. Consequently, the motionless mummified aphids must occur in such places where they are not damaged, if the parasite is to survive

the unsuitable period. When we exclude the natural mortality during quiescence, it is apparent that the parasites require stable conditions of the environment for survival. Hibernation sites and also aestivation sites of parasites can mostly be found at the same places where the chronic foci are during the year. This is a basic statement for parasite protection in cultivated areas; in some cultivated habitats, in annual crops namely, the parasites do not hibernate, while doing so in perennial crops. Aestivation of parasites can take place both in temporary and chronic foci. Hence the differences in cereal, potato and alfalfa fields.

As the occurrence of parasite quiescent states varies in accordance with distribution, due to a different climate and to peculiarities in aphid biology, the foci play a different role in this respect as well.

ROLE OF HOST SPECIFICITY. Various species of parasites are found in the foci. They naturally exhibit a different host range.

In the foci, the parasite species have various relations to a given aphid species, there may be a complex of parasites present in a focus, consisting of a single to several parasite species. Some parasites are strictly specialized, others can attack several host aphids. Host range can influence also the relations of the foci to the neighbourhood (habitats of a similar kind). Species with a wider host range usually disperse farther due to their ability to find other hosts in the neighbourhood, while strictly specialized parasites are closely dependent on their host's occurrence and dispersal. The influence of host specificity may exhibit variations with respect to distribution.

Examples may be found in the review of foci as well as in the introductory parts of this chapter.

PARASITE DISPERSAL. Dispersal of parasites from the foci as well as the infestation of aphids present there are the main features of parasites with respect to the research of foci.

Several factors seem to influence the dispersal of parasites from the foci, which are closely mutually connected.

1. **Host specificity.** Strictly specialized parasites are mutually fully dependent on their adaptation to the life-cycle of their host, while widely specialized parasites exhibit less dependence in accordance with their host range. Besides the host range, another specific feature, i.e. host instar preference plays an important role. Some parasites prefer lower instar aphids, which are then killed before reaching maturity, while others prefer higher instars. The latter results in killing the aphid in an adult stage, either alate or apterous. The alate parasitized aphids are able to disperse in the usual way, carrying thus the parasites to the new districts. This kind of parasite dispersal may sometimes be important in the dispersal from parasite foci as well, in California, e.g., the mode of dispersal influences the distribution of parasites of *Therioaphis trifolii* on alfalfa as *Praon exoletum* disperses mostly via alate aphids, while *Trioxys complanatus* kills the aphids before their reaching maturity, being thus slower in dispersal from its foci.

2. **Host searching behaviour.** Some parasites are capable of finding their hosts at a very low level of density, the other parasite species find their host only after its colonies have become larger. These specifically dependent features of searching behaviour also partially determine their ability to disperse and find their hosts in the neighbourhood of foci.

3. **Habitat.** As is apparent from the aforementioned observations, there is a generally different situation of parasite dispersal from the foci in case of annual and perennial

crops, namely in fields, which exhibit very special features, being influenced by cultivation to a comparatively higher degree than the forest habitats.

In the fields, in annual crops, the parasite foci on uncultivated land, meadows, pastures, roadsides, etc., are really the only foci of parasites from where they can disperse to the adjacent areas of cultivated annuals. This feature has been well known to various authors (e.g. TELLEGA, 1950), being confirmed by our numerous observations as well, that the aphids that disperse early in the season to young plants of annual crops are attacked first and mostly in the neighbourhood of waste places, roadsides, etc., i.e. in places which were later recognized as including chronic foci of parasites. This means that dispersal of aphids in the case of annual crops is apparently much more powerful as to the areas covered than that of parasites, which disperse only gradually from their foci. This movement is rather important for the evaluation of parasites in aphid limitation and control on annual crops, in control of aphids—vectors, etc. The example of *Aphis fabae* on sugar beet illustrates the point.

In perennial crops there is another situation, due to the more stable character of these communities; as a part of the chronic foci of parasites is often included just in the crop fields, the chronic foci of parasites are therefore practically identical with the whole cultivated crop plot. There is no need for parasites to disperse into the crop from the neighbourhood, as they can occur in foci in the field itself throughout the season. This does not mean naturally that there are no other chronic foci in the neighbourhood from which the parasites disperse to the field, but their significance is not as primary as in the case of annual crops.

4. Aphid life-cycle. Due to the strict habitat dependence, in a temperate zone for example, the parasites disperse from the foci to the neighbouring habitats of the same or a similar kind (forest-forest, steppe-steppe), while a certain part of aphids, i.e. the dioecious species, exhibit quite an opposite feature in alternating the habitats of different types during the season (Fig. 291). Naturally, some parasite species are also of intermediate character, in the arid zone namely, where the conditions are rather specific.

5. Density dependence is a significant factor in inducing parasite dispersal (WAY, 1966). There is no doubt that the population density conditions which occur in the foci will evidently basically influence the dispersal of parasites to neighbouring habitats of a similar kind. For the time being we have no detailed records at hand, however, such a research topic should be dealt with in the future to enable the classification of certain unknown aspects of the role of the foci.

6. Seasonal coincidence of host and parasite will apparently have a certain role in parasite dispersal as well. In cases of good adaptation, i.e. in cases of good seasonal coincidence, the parasite dispersal from the foci may be expected to be density dependent, with respect to the given host species. In widely specialized parasites, which are naturally less seasonally dependent on one host species due to the occurrence of various hosts in the same habitat, the density dependence can be obscured by the seasonal occurrence of several host aphids with a corresponding influence of parasite dispersal. For example, in case of a dioecious aphid species, such as *Aphis fabae* in C. Europe, the aphid migrates in late spring from certain shrubs to sugar-beet and to other herbs in field habitats. However, in a roadside or a meadow the parasites have attacked a number of other aphids since early spring, and their density will not primarily depend on the number of immigrating *A. fabae* but on the density of other aphids present earlier in the habitat. Seasonal coincidence, in this case, is primarily not density dependent as to the occurrence of *A. fabae* in the field habitats, dispersal of the parasite *Lysiphlebus fabarum* from roadsides to sugar beet fields will possibly depend primarily on the density of populations of aphid species occurring in the

H	PHP	SHP	PHP
P	A _{PC}	B _{PC}	A _{PC}

Fig. 291. Relation of sources of aphids and foci of parasites.

1. Host aphid dioecious, primary et secondary host plants in different kinds of habitats. Parasite complexes different.

H	PHP	SHP	PHP
P	A _{PC}	+	B _{PC}

2. Host aphid dioecious, primary et secondary host plants in intermediate kinds of habitats. Parasite complexes mixed.

H	HP
P	A _{PC}

3. Host aphid monoecious, Parasite complexes identical perennially. HP – Host Plant, PHP – SHP Primary or Secondary Host Plants, H – Host, P – Parasite, A_{PC}, B_{PC} – A and B parasite complexes.

roadsides, not on the density of *Aphis fabae* immigrating to the sugar-beet field. The high population density of *A. fabae* may naturally cause secondarily the density dependent influence on the parasite populations and their dispersal from the roadside habitat as well.

SOURCES OF APHIDS. The basic relation between the aphid and parasite is in that they are two different groups of insects, there existing a host-parasite relationship between them, the result of a long evolution. The relations to the environment depend on each of the groups mentioned, exhibiting a various degree of similarity or dissimilarity. This statement is quite true as to the foci of aphids and parasites. To avoid possible misinterpretation, we decided to use the terms "sources" for the aphids and "foci" for the parasites although both words are synonymous as to their primary meaning.

The basic difference between both groups with respect to sources or foci seems to be the habitat dependence, dispersal, and associated role of parasite specificity.

As already mentioned, habitat dependence exhibits special features in some groups of aphids (dioecious species) in that they alternate the kinds of habitats due to their obligatory host alternation as a part of the life cycle. The parasite biology is different; they are attached to a given kind of habitat. The above scheme illustrates the dependence of some sources of aphids and foci of parasites. (Fig. 291).

Many examples of this scheme can be found in various chapters of this book.

Microhabitat dependence is also important. Microclimatic conditions inside the

habitat, mode of host life, can cause the difference between the occurrence of aphids and parasites.

Mode and power of dispersal is also different in both groups. Aphids generally disperse more powerfully, while the parasite dispersal is mostly gradual and relatively low except the cases when the parasite developmental stages are transferred to new districts inside alate parasitized aphids.

Host range of parasites is another feature that can basically distinguish the sources of aphids and foci of parasites. In addition to its role in habitat dependence, host specificity of parasites can determine also their microhabitat distribution. Regarding the host range, the foci can be further differentiated with respect to the occurrence of separate host aphids even in the same kind of habitat. An illustrative example is as follows: In C. Europe, the main foci of *Aphidius ervi* are certainly alfalfa fields (host: *Acyrtosiphon pisum*), *Sarothamnus scoparius* shrubs (host: *Acyrtosiphon spartii*) in hedges, and *Urtica dioica* growths (host: *Microlophium evansi*). Each of these hosts is differentiated as to the microhabitat (host plant occurrence), however, the parasite is able to occur in all these places and disperse from a focus associated with the source of one aphid to a source of another aphid, a feature the aphids cannot follow due to different host specificity and microhabitat requirements. An absolutely contrary example may be found in some cases of strictly specialized parasites, which—due to their restricted original host range—are unable to follow their host in all the micro-environments in a district (*Therioaphis trifolii* and its parasites in California).

APHID OUTBREAKS. Various authors have shown that outbreaks may occur both in natural (or almost natural) and cultivated environments. Beech forests with common outbreaks of *Phyllaphis fagi*, and *Aphis fabae* on sugar beet may be mentioned as examples from C. Europe. There is, however, no doubt that outbreaks are more common with cultivated crops than in natural stands. The diversity of plant cover and associated insect species in general are believed to have the determining role. Foci of aphid parasites are naturally just typical of those occurring in such stands with diversity of species, while they may be absent or rare in cultivated crops. As the absence of parasite foci means the absence of a limiting agent as well, the pest aphid outbreak possibility in the crop is naturally apparent. There is no doubt that the presence of parasite foci inside or near the cultivated crops can prevent the aphid outbreaks in case the parasites are at least partially effective and the community exhibits a certain degree of stability. The role of the presence of chronic parasite foci in preventing aphid outbreaks in cultivated crops was shown experimentally by Californian authors (V. D. BOSCH, HAGEN, SCHLINGER, R. F. SMITH, etc.) in developing the strip cutting alfalfa program, the main task being to conserve, at least partially, the stable character of the alfalfa field ecosystem.

APHIDS-VECTORS. The transmission of virus diseases of plants by aphids and resulting damage to the plants is nowadays, in many cases, much more important than the damage caused to plants by sucking.

The significance of aphid sources for the spread of virus diseases was observed by many authors. Of these, two should be reviewed here to show the specificity of each different case:

DAIBER (1962, 1964), when dealing with the problem of control of potato aphids and spread of virus diseases of potatoes in S. Africa found that the apterous aphid populations were practically eliminated by systemic insecticides on potatoes. But the winged aphids were still able to enter the treated plots and could transmit the virus under favourable conditions. Therefore, a systemic insecticide was not capable of

killing the aphids before they could transmit the virus. Moreover, when searching for the sources of pest aphids, this author found that irrigated gardens with many host plants are perennial sources of potato pest aphids, they are important because of the high dispersal of alate aphids and thus indirectly dangerous for leaf rolls spread as the winged aphids originating from garden potatoes may initiate colonization in field potatoes and simultaneously spread the virus.

As almost a contrary opinion to the mentioned paper, the research results of RIBBANDS (1964) can be mentioned here. This author, when dealing with the control of certain virus diseases of sugar beet in Great Britain, found that *Myzus persicae*, a predominant vector of sugar beet virus disease, overwinters mainly on cultivated secondary host plants that are not associated with viruses. The viruses overwinter mainly on sugar beet, which are the main source of infestation the following summer, weeds being considered unimportant.

Generally, it is well known that the parasites are partially effective species, which can sometimes limit the host occurrence to a certain degree, although they rarely almost eliminate the population of an aphid in a certain plot. With respect to the transmission of viruses by aphids it is obvious that a small number of virus vectors is sufficient to cause damage to plants through disease transmission, while the parasites are not capable of preventing the emigration of so many aphids from one plant to another, they, nevertheless may partially limit this number. From this point of view the significance of parasite foci in checking aphid vectors must be considered, too.

WEED PLANTS. Weeds are common guides of man's agriculture. They spread accidentally over the world due to the activity of man, many of them becoming cosmopolitan in distribution. They, as a group, exhibit rather a wide adaptability to various environments and are typical just by their survival and ability to compete successfully with other plants.

Weed plants belong to different groups of plants. Many of them are attacked by various aphid species, while others are infested by a more or less specialized aphid fauna. The features mentioned clearly show that weeds apparently represent important sources of host aphids with respect to the parasites. Due to their common occurrence, they represent important food sources for parasites and probably for other natural enemies as well.

Generally, we divide the weed plants into several groups:

1. Weeds attacked by pest aphids,
2. Weeds attacked by economically indifferent aphids,
 - (a) indifferent aphids are alternative hosts of parasites of pest aphids,
 - (b) indifferent aphids are hosts, either main or alternative, of economically indifferent aphid parasites.

The above division of weed plants clearly shows that in no case may the weeds be put into one group. For example, PEAIRS (1947—see below) classified generally all the weeds as being noxious everywhere. Similarly, SHANDS et al. (1963, 1964) proposed the elimination of weeds both in uncultivated or crop land as they support large populations of pest aphids that attack potatoes later in the season. Other authors have classified weeds as useful plants because of natural enemy conservation.

BOMBOSCH (1966) briefly reviewed the various opinions and showed, in accordance with research of aphid predators—the syrphid flies—that in no case may all the weeds be accepted as useful from this point of view.

Several examples of weed plants and associated aphid and parasite fauna of C. Europe can be mentioned as an illustration, while some other examples are found in the review of foci:

Aretium sp. - *Aphis fabae*: *Praon abjectum*, *Trioxys angelicae*, *Lysiphlebus fabarum* (pest aphid) *Brachycaudus cardui*: *Lipolexis gracilis*, *Lysiphlebus fabarum*, *Paralipsis cuervis* (pest aphid); *Chromaphis* sp.: *Lysiphlebus fabarum*, *Paralipsis cuervis* (useful alternative host).

Centaurea spp. - *Dactynotus jaceae* et sp.: *Praon dorsale*, *Trioxys centaureae* (almost indifferent species); *Macrosiphoniella stägeri*: *Praon dorsale*, *Ephedrus campestris* (indifferent species).

Chenopodium spp. - *Aphis fabae*: *Lysiphlebus fabarum*, *Ephedrus plagiator* (pest species); *Myzus persicae*: *Diaeretiella rapae* (pest species); *Hayhurstia atriplicis*: *Ephedrus nucheri*, *Diaeretiella rapae* (practically useful alternative host).

Cichorium intybus. - *Aphis intybi*: *Lipolexis gracilis*, *Lysiphlebus fabarum* (useful alternative host); *Dactynotus cichorii* (indifferent species).

Cirsium arvense. - *Aphis fabae*: *Lipolexis gracilis*, *Lysiphlebus fabarum*, *Trioxys angelicae* (pest species).

Sonchus oleraceus. - *Hyperomyzus lactucae*: *Aphidius souchi*, *Lysiphlebus fabarum*, *Praon volucre* (pest).

Taraxacum officinale. - *Aphis taraxacicola*: *Lipolexis gracilis*, *Lysiphlebus fabarum* (useful alternative hosts).

Aphid fauna of separate weeds can be varied in different areas or the same aphid species may have various economic significance. For example, *Sonchus oleraceus* is attacked by *Hyperomyzus lactucae* both in Europe and in Cuba, in Europe, it is a secondary host plant of a pest aphid that attacks *Ribes*, while in Cuba, due to the absence of *Ribes* and tropical climate peculiarities, the aphid has no economic importance, being attached exclusively to *Sonchus*.

- *Undergrowth of orchards*. Weeds in orchards may be host plants of alternative hosts of parasites of orchard pest aphids, or they may be hosts of aphids attacked by parasites that have no relation to fruit trees. In some cases, too, they may represent host plants of orchard pests. Examples are given in the review of foci.

Mostly, weeds in orchards represent temporary foci of parasites. Clean cultivation program and the problem of undergrowth in orchards must be dealt with in accordance with specific requirements with respect to fruit trees grown and geographic peculiarities.

- *Crop fields*. Weed plants in crop fields are generally classified as noxious and they are eliminated through herbicide treatment. It seems that their possible usefulness in parasite conservation would not compensate for the damage caused to economic crops. In addition, the record of UVAROV (1964, after WOLCOTT, 1928) should be mentioned, dealing with aphids as vectors of sugar cane diseases. According to this record, *Rhopalosiphum maidis*, the vector of the mosaic disease of the sugar cane, is forced to move to cane when wild grasses are removed by weeding. This would perhaps show that weeding would not protect the sugar cane from diseases transmitted by the aphid. According to our studies undertaken in Cuba in 1965, *Rh. maidis* occurs commonly on Indian corn and various other grasses, both wild and cultivated, including sugar cane. Weeding apparently would not have any significance with respect to the transmission of disease as there are numerous sources of aphids in sugar cane field neighbourhood from which they can disperse to cane and transmit the disease. Biological control of the aphid could perhaps be at least partially useful, although it cannot also eliminate the aphid vectors.

- *Meadows and similar habitats*. Weed plants can also be found to be represented to a various degree in meadows and related habitats. With them both economically indifferent aphids and pest species may be found being parasitized by various aphidid parasites. The heterogeneous plant cover, the dispersal of plants attacked by aphids,

and the presence of parasites allow us to consider meadows as habitats including many temporary foci and chronic foci of parasites. Weed plants, if not too numerous, do not seem to cause any serious economic damage; if they are infested by pest aphids which disperse from there to crop fields, the diversity of the community seems to be well balanced and the aphids are limited by parasites. Examples are given in the review of foci.

- *Ruderals*. Weeds are typical members of ruderal flora associated with waste places and allied habitats. In ruderals, weeds do not cause direct damage to field crops except for the dispersal of seed. According to SCHWARZ (1959), certain weed plants can be of importance as sources of virus diseases, which could be transmitted by aphids emigrating from ruderals to crop fields. Generally, ruderals exhibit perhaps the most numerous and rather heterogeneous aphid fauna, associated with various parasite species. These features, and the omitting of such areas by man, make valuable chronic foci of parasites from ruderals, both of economically useful and indifferent species. The rather heterogeneous plant cover and diversity of aphid species permit us to presume that if pest aphids occur in such places and there are many such cases, they will be heavily parasitized. Field observations, although hardly of any importance economically, show this opinion to be justified. Examples again are in the review of foci.

- *Diversity of plant cover*. PIMENTEL (1961, etc.) and other authors mentioned earlier have shown that the diversity of species is characterized for mixed species plantings or complex communities, while simple communities have a less stable community balance. The presence of weed plant increases the diversity of plant cover. However, in certain plots, i.e. economic crop fields, just strict monocultures are required.

As weed plants are eliminated in field crop areas, the diversity of plant cover must be repaired, just in neighbouring habitats for the purpose of parasite conservation. Weed plants could represent valuable elements of diversity of such plant communities, which could be useful due to their incidental dispersal, occurrence and associated fauna. Examples are mentioned in the review of foci.

- *Clean culture concept*. PEARS (1947), when dealing with the control of insect pests in agriculture, proposed the clean culture concept, which includes also the "destruction of weeds and hedgerows in the neighbourhood of crop areas". This concept was discussed by PIMENTEL (1961); in his studies on species diversity and population outbreaks he arrived at the conclusion that hedgerows, including weeds and plants of many kinds, may provide diversity with additional species of insects which when added to the community of sterile crop fields increase its stability.

As already shown, we must classify the weeds separately and not include them all under "noxious" plants. For this reason, we can consider PIMENTEL's conclusions to be quite correct.

- *Biological control of weeds*. According to the proposal of HEINZE (1956) strictly specialized aphids can be used in biological control of weeds. The attacked host plants, i.e. weeds, need not be destroyed due to aphid sucking; because of being weakened they are not expected to be capable of competing with other plants. Aphids as vectors of certain diseases might be also used for such purposes. Several projects have been elaborated by HEINZE, such as introduction of *Macrosiphoniella* sp. in control of *Galinsoga parviflora* weed in Europe, or *Dactynotus erigeronensis* in control of *Erigeron canadensis*.

Biological control of weeds is not included in the scope of this book, however, according to our opinion we can expect that both *Macrosiphoniella* sp. and *Dactynotus erigeronensis* will be attacked soon by indigenous parasites in Europe in a similar way as the European aphids of these genera, as the parasites attacking such groups of

aphids include a number of Dactynotine aphids in their host specificity range. From this point of view, although the European parasites of *Dactynotus* and *Macrosiphoniella* species are practically indifferent, the same parasites would exhibit adverse effects in case of weed control by introduced aphids into Europe and their foci would be harmful instead of indifferent. Nevertheless, also in this case, elimination of *Achillea* or *Artemisia* weeds is not possible in Europe, neither is the elimination of associated aphids and parasites, so that introduction of the above mentioned aphids could fail, just due to the action of European parasites of related aphid species.

REVIEW OF EXAMPLES. The main purpose of this review is to give the reader a well-documented example of research of parasites with respect to their foci in nature. Naturally, it is impossible to cover all the geographic distribution area of the aphidiids. This is one of the aims of interested workers in separate countries, who may enjoy this kind of work. Besides, we have personally visited only some districts and zones, so that a "general" classification would be artificial if elaborated, not to speak of the fact that we are more or less at the beginning of a more detailed work on the ecology of the aphidiids as a whole. In connection with our research work undertaken in Czechoslovakia—a relatively very small area—for about 10 years, it is necessary to stress the time consuming process before a worker can gain sufficient field experience, necessary for the research of parasite foci. Having the above mentioned ideas in mind, we have selected a certain number of examples from very different areas in which, besides others, we have undertaken some detailed research: C. Europe, S. Europe, Caucasus, C. Asia, and Cuba. In these cases, too, not all but only some types of the landscape are dealt with, attempting, on the one hand, to show the praxis and results of such research work, on the other hand, to bring examples from different zones to permit the reader to acquire at least a brief orientation as to the corresponding peculiarities as well. General notes on separate habitats have mostly been omitted, the "interrelations" and "classification" being made on the basis of a greater number of examples studied in the separate areas mentioned. More detailed information on the foci in separate countries may be found in various papers of the author (see: References).

— CENTRAL EUROPE.

— *Coniferous forest.* Aphids: *Buchneria pectinatae* — *Abies alba*, *Cinara* spp. — *Picea excelsa*, *Larix decidua*, *Pinus* spp., *Cupressobium juniperi* — *Juniperus communis*, *Lachnilla costata* — *Picea excelsa*, *Liosomaphis abietina* — *Abies alba*, *Protolachnus agilis* — *Pinus silvestris*, *Schizolachnus pineti* — *Pinus silvestris*, *Todolachnus abieticola* — *Abies alba*. Parasites: *Diaeretus leucopterus* — *Protolachnus agilis*, *Lysaphidius schimitscheki* — *Liosomaphis abietina*, *Metaphidius aterrimus* — *Cinara* spp., *Pauesia abietis* — *Cinara laricis*, *Cinara* spp., *Pauesia cupressobii* — *Cupressobium juniperi*, *P. grossa* — *Todolachnus abieticola*, *Pauesia infusata* — *Buchneria pectinatae*, *Pauesia juniperorum* — *Cupressobium juniperi*, *Pauesia laricis* — *Cinara* spp., *Pauesia piceaeacollis* — *Cinara* spp., *Pauesia pini* — *Cinara* spp., *Pauesia silvestris* — *Cinara* spp., *Pauesia milachni* — *Schizolachnus pineti*, *Praon bicolor* — *Protolachnus agilis*. Coniferous forest parasite fauna represents a strictly specialized group that has no relation to other habitats. Nevertheless, there are mixed forests very commonly found in C. Europe, and, also in this case the aphids associated with conifers, as well as their parasites, are always rather specific. Chronic foci of parasites are included in coniferous forest habitats.

— *Deciduous forest.* Aphids: *Acyrtosiphon caraganae* — *Caragana arborescens*, *Anoecia* spp. — *Cornus sanguinea*, *Aphis cognatella* — *Euonymus europaea*, *Aphis craccivora* — *Robinia pseudoacacia*, *Caragana arborescens*, *Aphis fabae* — *Euonymus europaea*, *Aphis farinosa* — *Salix* spp., *Aphis idaei* — *Rubus idaeus*, *Aphis nasturtii* — *Rhamnus*

cathartica, *Aphis pomi* - *Malus silvestris*, *Crataegus monogyna*, *Aphis sambuci* - *Sambucus nigra*, *Aphis schneideri* - *Rubus* sp., *Aphis spiraeophaga* - *Spiraea* sp., *Aphis viburni* - *Viburnum opulus*, *Brachycandus cardui* - *Prunus spinosa*, *Brachycandus helichrysi* - *Prunus spinosa*, *Calaphis* spp. - *Betula* sp., *Callaphis juglandis* - *Juglans regia*, *Cavariella* spp. - *Salix* sp., *Ceruraphis eriophori* - *Viburnum opulus*, *Chaitophorus* spp. - *Populus* spp., *Chromaphis juglandicola* - *Juglans regia*, *Cryptomyzus ribis* - *Rubus* spp., *Drepanosiphum platanoides* - *Acer* spp., *Dysaphis* spp. - *Malus silvestris*, *Crataegus monogyna*, *Sorbus torminalis*, *Prus communis*, *Eucallipterus tiliae* - *Tilia* spp., *Glyphina betulae* - *Betula* sp., *Hyadaphis inellifera* - *Lonocera xylocetum*, *Hyalopterus pruni* - *Prunus spinosa*, *Hyperomyzus lactucae* - *Rubus* spp., *Kallistaphis betulicola* - *Betula* sp., *Liosomaphis berberidis* - *Berberis vulgaris*, *Macrosiphum sinestum* - *Rubus* sp., *Macrosiphum rosae* - *Rosa* spp., *Myzaphis rosarum* - *Rosa* spp., *Myzocallis carpini* - *Carpinus betulus*, *Myzocallis coryli* - *Corylus avellana*, *Myzus cerasi* - *Prunus avium*, *Myzus ligustri* - *Ligustrum aviculare*, *Nectarosiphum rubi* - *Rubus* sp., *Passerina tetrahoda* - *Rosa* sp., *Periphyllus villosus* - *Acer* spp., *Phorodon humuli* - *Humulus lupulus*, *Prunus* sp., *Phyllaphis fagi* - *Fagus silvatica*, *Prociplus fraxini* - *Fraxinus excelsior*, *Pterocomma pilosum* - *Salix caprea*, *Pterocomma salicis* - *Salix amygdaluna*, *Pterocomma* spp. - *Populus* sp., *Salix* sp., *Rhopalosiphum padi* - *Padus racemosa*, *Roeplca marchali* - *Prunus mahaleb*, *Schizoneura ulmi* - *Ulmus campestris*, *Stomaphis quercus* - *Quercus* sp., *Symydobius oblongus* - *Betula* sp., *Thelaxes dryophila* - *Quercus* sp., *Timocallis platani* - *Ulmus* sp., *Tuberculoidea annulatus* - *Quercus* sp. Parasites: *Aphidius caraganae* - *Acyrtosiphon caraganae*, *Aphidius cingulatus* - *Pterocomma pilosum*, *P. salicis*, *P. spp.*, *Aphidius hortensis* - *Liosomaphis berberidis*, *Aphidius ribis* - *Cryptomyzus ribis*, *Aphidius rosae* - *Macrosiphum rosae*, *Aphidius rubi* - *Macrosiphum sinestum*, *Aphidius salicis* - *Aphis farinosa*, *Cavariella* spp., *Aphidius setiger* - *Periphyllus villosus*, *Aphidius saccatus* - *Calaphis* sp., *Areopraon lepellei* - *Schizoneura ulmi*, *Dyscritulus planticeps* - *Drepanosiphum platanoides*, *Ephedrus lacertosus* - *Macrosiphum rosae*, *Rhopalosiphoninus* sp., *Ephedrus minor* - *Myzaphis rosarum*, *Passerina tetrahoda*, *Ephedrus persicae* - *Aphis fabae*, *Aphis idaei*, *Brachycandus* sp., *Dysaphis devector*, *D. sorbi*, *D. spp.*, *Hyadaphis inellifera*, *Myzus ligustri*, *Myzus cerasi*, *Phorodon humuli*, *Rhopalosiphum padi*, *Roeplca marchali*, *Ephedrus plagiator* - *Acyrtosiphon caraganae*, *Aphis fabae*, *A. farinosa*, *A. idaei*, *A. nasturtii*, *A. pomi*, *A. spiraeophaga*, *A. spp.*, *Brachycandus cardui*, *B. spp.*, *Ceruraphis eriophori*, *Capitophorus* sp., *Dysaphis devector*, *D. sorbi*, *D. spp.*, *Hyalopterus pruni*, *Hyperomyzus lactucae*, *Liosomaphis berberidis*, *Macrosiphum rosae*, *Myzocallis coryli*, *Myzus cerasi*, *Phorodon humuli*, *Prociplus fraxini*, *Rhopalosiphum padi*, *Schizoneura ulmi*, *Lysiphlebus ambiguus* - *Aphis farinosa*, *A. schneideri*, *Lysiphlebus salicaphis* - *Chaitophorus* spp., *Lysiphlebus thelaxi* - *Thelaxes dryophila*. Monotoxins cerasi - *Myzus ligustri*, *Monotoxus pseudoplatani* - *Drepanosiphum platanoides*, *Praon abjectum* - *Aphis craccivora*, *A. fabae*, *A. farinosa*, *A. sambuci*, *A. viburni*, *Rhopalosiphum padi*, *Praon flavinode* - *Eucallipterus tiliae*, *Myzocallis carpini*, *Timocallis platani*, *Tuberculoidea annulatus*, *Praon rosaeola* - *Macrosiphum rosae*, *Praon volucre* - *Acyrtosiphon caraganae*, *Aphis craccivora*, *Dysaphis* sp., *Hyalopterus pruni*, *Macrosiphum rosae*, *Protaphidius wismanii* - *Stomaphis quercus*, *Toxares deltiger* - *Acyrtosiphon caraganae*, *Trioxys acalephae* - *Aphis craccivora*, *A. farinosa*, *A. spiraeophaga*, *Trioxys angelicae* - *Acyrtosiphon caraganae*, *Aphis cognatella*, *A. craccivora*, *A. fabae*, *A. farinosa*, *A. pomi*, *A. sambuci*, *A. spiraeophaga*, *A. viburni*, *Ceruraphis eriophori*, *Dysaphis devector*, *D. sp.*, *Rhopalosiphum padi*, *Trioxys cirsti* - *Drepanosiphum platanoides*, *Trioxys falcatus* - *Periphyllus villosus*, *Trioxys hortorum* - *Timocallis platani*, *Trioxys pallidus* - *Chromaphis juglandicola*, *Eucallipterus tiliae*, *Myzocallis carpini*, *Tuberculoidea annulatus*, *Triaxys phyllaphidis* - *Phyllaphis fagi*. Similarly, as with the coniferous forest, the deciduous forest also exhibits strong peculiarities. Nevertheless, there can be distinguished two groups of aphids and more

or less the same of parasites: the first group, represented mainly by the Callaphidid and Chaitophorid aphids, etc., includes the true forest species, which are monoeccious and occur in forest habitats throughout the whole year. The second group represented by a number of aphids (Myzine, Aphidine, Pemphigine species, etc.) is composed of species which are either monoeccious or dioecious, the latter are therefore only temporary inhabitants of the deciduous forest habitats, as they migrate during the season to steppe type habitats, attacking various herbs there. Species of the latter group may cause damage both to the forest trees (*Myzus cerasi*) or to the herbs (*Aphis fabae*). Contrary to the aphids, the sources of which in deciduous forests are either chronic or temporary, the foci of parasites are only of the chronic type. Mostly strictly forest species are present in the fauna of parasites of deciduous forest habitats (parasites of Callaphidid and Chaitophorid aphids namely), nevertheless, due to the common intermediary character of clearings, edges of woods, shrubs, some species of parasites may exhibit also intermediary features as to the habitat dependence.

- *Forest undergrowth*. Aphids: *Amphorophora ampullata* - *Dryopteris austriaca*, *Anilacorthum dryopteridis* - *Dryopteris austriaca*, *Anilacorthum chelidonii* - *Chelidonium majus*, *Anilacorthum geranii* - *Erodium cicutarium*, *Geranium affine*, *Anilacorthum sp.* - *Geranium robertianum*, etc., *Cavariella spp.* - *Angelica silvestris*, *Anthriscus silvestris*, *Impatiens balsamines* - *Impatiens noli-tangere*, *Linosisiphon galiophagus* - *Galium silvaticum*, *Macrosiphum daphnoides* - *Daphne mezereum*, *Macrosiphum gei* - *Geum sp.*, *Macrosiphum prenanthidis* - *Prenanthes purpurea*, *Macrosiphum stellariae* - *Stellaria holostea*, *Nasonovia nigra* - *Hieracium silvaticum*, *Nasonovia pilosellae* - *Hieracium pilosella*, *Nasonovia ribisnigri* - *Hieracium spp.*, *Rhopalosiphonium sp.* - *Oxalis acetosella*, *Sitobium equiseti* - *Equisetum silvaticum*. Parasites: *Aphidius equiseticola* - *Sitobium equiseti*, *Aphidius hieraciorum* - *Nasonovia nigra*, *N. pilosellae*, *N. ribisnigri*, *Aphidius loniceriae* - *Amphorophora ampullata*, *Anilacorthum dryopteridis*, *Macrosiphum daphnoides*, *M. gei*, *M. prenanthidis*, *M. stellariae*, *Aphidius matricariae* - *Linosisiphon galiophagus*, *Aphidius nigrescens* - *Anilacorthum geranii* and *spp.*, *Ephedrus lacertosus* - *Rhopalosiphonium sp.*, *Ephedrus minor* - *Cavariella spp.*, *Ephedrus plagiator* - *Anilacorthum chelidoni*, *A. spp.*, *Macrosiphum prenanthidis*, *Monoctonus angustivalvus* - *Nasonovia nigra*, *Monoctonus caricis* - ? *Monoctonus crepidis* - *Nasonovia spp.*, *Monoctonus nervosus* - *Impatiens balsamines*, *Praon pubescens* - *Nasonovia nigra*, *N. ribisnigri*. Forest undergrowth has generally rather similar features irrespective of the type of forest, only pine forests seem to exhibit certain differences. Two groups of species seem to be recognizable: the one includes typical species of the forest undergrowth which have no relation to the aphids living on trees and shrubs: *Aphidius hieraciorum*, *A. loniceriae*, *A. nigrescens*, *Monoctonus angustivalvus*, *M. crepidis*, *M. nervosus*, *Praon pubescens*, etc. The second group includes species which attack the different aphid species living in the undergrowth and on the deciduous trees and shrubs: *Ephedrus plagiator*, *E. minor*, etc. Therefore, in the deciduous forest there may be certain relations between the tree and shrub strata and the undergrowth with respect to aphid parasites, while this is not the case in coniferous forests, where the parasites attacking aphids on trees and in undergrowth are strictly separated groups.

- *Peat bogs*. Peat bogs exhibit a rather specialized fauna of aphids and associated parasites. Partially there are also represented various species connected with the occurrence of *Pinus* or *Betula* in the bogs. *Diaretellus* species form a typical complex associated with aphids attacking mosses. They are rather specialized and economically almost indifferent. *Rhopalosiphum nymphaeae* seems to be the only economically important aphid, which finds its secondary host plants in peat bogs, being a pest on its primary host plants, the *Prunus* trees. In peat bogs, it is attacked by a specialized parasite *Praon necans*, which seems to have its foci in these places.

– Orchards and orchard avenues. Aphids: *Allocataphis quaestionis* – *Malus silvestris*, *Aphis idaei* – *Rubus idaeus*, *Aphis pomi* – *Malus silvestris*, *Brachycandus cardui* – *Prunus domestica*, *Brachycandus helichrysi* – *Prunus domestica*, *P. persica*, *Callaphis juglandis* – *Juglans regia*, *Chromaphis juglandicola* – *Juglans regia*, *Cryptomyzus ribis* – *Ribes rubrum*, *Dysaphis devector* – *Malus silvestris*, *Dysaphis* spp. – *Pirus communis*, *Malus silvestris*, *Hyalopterus pruni* – *Prunus domestica*, *P. persica*, *P. armeniaca*, *Hyperomyzus lactucae* – *Ribes nigrum*, *Myzus cerasi* – *Prunus avium*, *P. cerasus*, *Myzus persicae* – *Prunus armeniaca*, *Nectarosiphon rubi* – *Rubus idaeus*, *Phorodon humuli* – *Prunus domestica*, *Rhopalosiphon nymphaeae* – *Prunus domestica*, *P. persica*, *P. armeniaca*, *Schizoneura ulmi* – *Ribes* sp. (roots). Parasites: *Aphidius matricariae* – *Myzus cerasi*, *Aphidius ribis* – *Cryptomyzus ribis*, *Ephedrus cerasicola* – *Myzus cerasi*, *Ephedrus persicae* – *Allocataphis quaestionis*, *Aphis idaei*, *Brachycandus helichrysi*, *Dysaphis devector*, *D. sp.*, *Myzus cerasi*, *Phorodon humuli*, *Ephedrus plagiator* – *Aphis idaei*, *A. pomi*, *Brachycandus cardui*, *Dysaphis devector*, *D. spp.*, *Hyalopterus pruni*, *Hyperomyzus lactucae*, *Myzus cerasi*, *Phorodon humuli*, *Lipolexis gracilis* – *Brachycandus helichrysi*, *Myzus cerasi*, *Praon volucre* – *Dysaphis* sp., *Hyalopterus pruni*, *Trioxys angelicae* – *Aphis pomi*, *Brachycandus helichrysi*, *Dysaphis devector*. The fauna of orchard undergrowth is practically represented by the meadow and ruderal elements (see below). Orchard habitats exhibit many features of forest-type habitats, however, the general character is somewhat of intermediate type due to the existence of undergrowth, where many species of steppe-character may be found as well. Generally, there are either perennially (*Aphis pomi*) or seasonally present species (*Dysaphis devector*, *Hyalopterus pruni*, *Myzus cerasi*, etc.), the sources of aphids being therefore chronic or temporary. As orchards and avenues represent perennial communities of a forest type, the foci of parasites are of the chronic type. Nevertheless, due to the selection of plant species grown, there may be a seasonal lack of certain aphids, and this may force the parasites to search for the hosts in the orchard neighbourhood; for this reason, the composition of the orchard neighbourhood and interrelations of the habitats are evident. Similarly as in the deciduous forest, there may be chronic sources of aphid pests in orchards, from which they may disperse to other field crops and cause damage. This is the case of *Phorodon humuli*, *Myzus persicae*, *Hyalopterus pruni*, etc.

– Parks, shady tree avenues. These habitats are of forest type, although the composition of plants is mostly artificial. However, the greatest part of the plant species found here can be met with in nature as well; only a minor part of trees and shrubs are not found in a wild state, these species being mostly of exotic origin. The above conditions have a corresponding influence on the fauna of aphids and parasites which is identical to that of the corresponding types of forests. Similarly, only chronic foci of parasites can be found in parks.

– Hop gardens. Aphids: *Phorodon humuli*. Parasite: *Ephedrus plagiator*, *Trioxys humuli*. Hops are infested seasonally by *Phorodon humuli*, which has *Prunus* species as its primary host plant. Chronic foci are present in forest type habitats, the occurrence on hops is only of a temporary character. Because of the life cycle of the aphid and the presence of chronic foci of parasites, there are strong connections between the hop gardens and the neighbourhood, orchards, shrubs, and deciduous forests namely.

– Meadows. Aphids: *Acyrtosiphon pisum* – *Lathyrus* sp., *Medicago* spp., *Melilotus albus*, *M. officinalis*, *Trifolium* spp., *Vicia* spp., *Acyrtosiphon spartii* – *Sarothamnus scoparius*, *Anoecia* sp. – *Agropyrum repens*, *Aphis craccivora* – *Vicia sepium*, *V. cracca*, *Aphis craccivora* – *Medicago sativa*, *Onobrychis sativa*, *Trifolium* sp. *Vicia* sp., *Aphis euphorbiae* – *Euphorbia cyparissias*, *Aphis fabae* – *Cirsium* sp., *Chenopodium* sp., *Centaurea cyanus*, *Carduus* sp., *Campanula* sp., *Rumex* sp., *Urtica urens*, etc., *Aphis galii-sabini* – *Asperula cynanchica*, *Aphis myrsi* – *Cichorium intybus*, *Aphis*

laubersi – *Daucus carota*, *Aphis plantaginis* – *Plantago* spp., *Aphis poterii* – *Sanguisorba minor*, *Aphis roepkei* – *Potentilla reptans*, *P. anserina*, *Aphis rumicis* – *Rumex* sp., *Aphis salviae* – *Salvia* spp., *Aphis stachydis* – *Stachys recta*, *Aphis taraxacicola* – *Taraxacum officinale*, *Aphis thomasi* – *Scabiosa columbaria*, *Aphis urticae* – *Urtica dioica*, *U. urens*, *Aphis vanderghooi* – *Achillea millefolium*, *Aphis verbasci* – *Verbascum austriacum*, *Brachycaudus ballotae* – *Ballota nigra*, *Brachycaudus cardui* – *Carduus* spp., *Matricaria* sp., *Arctium* sp., *Brachycaudus helichrysi* – *Anthemis* sp., *Arctium* sp., *Brachycaudus lychnidis* – *Melandrium rubrum*, *Brachycaudus mordwilkoii* – *Eclium vulgare*, *Brachycaudus rumexicoleus* – *Rumex acetosella*, *Brachycaudus tragopogonis* – *Tragopogon pratense*, *Brevicoryne brassicae* – *Brassica* spp., *Cavariella* sp. – *Daucus carota*, *Colorado achilleae* – *Achillea millefolium*, *Colorado tanacetina* – *Tanacetum vulgare*, *Cryptosiphum artemisiae* – *Artemisia vulgaris*, *Dactynotus aeneus* – *Carduus* spp., *Dactynotus campanulae* – *Campanula* spp., *Dactynotus cichorii* – *Cichorium intybus*, *Crepis biennis*, *Centaurea cyanus*, *Leontodon hispidus*, *Lapsana communis*, *Dactynotus cirsii* – *Cirsium* sp., *Dactynotus jaceae* – *Centaurea jacea*, *C. scabiosa*, *C. stoebe*, *Dactynotus linariae* – *Aster linosyris*, *Dactynotus pictidis* – *Picris hieracioides*, *Dactynotus sonchii* – *Sonchus oleraceus*, *Dactynotus taraxaci* – *Taraxacum officinale*, *Dysaphis crataegi* – *Daucus carota*, *Dysaphis* spp. – *Arctium lappa*, *Galiobium laugei* – *Galium verum*, *Hayhurstia atriplicis* – *Atriplex* sp., *Chenopodium* sp., *Hyadaphis* sp. – *Conium maculatum*, *Hyadaphis hofmanni* – *Galium verum*, *Hyadaphis* sp. – *Galium verum*, *G. mollugo*, *Hyperomyzus lactucae* – *Sonchus asper*, *S. oleraceus*, *Linosophon asperulophagus* – *Asperula odorata*, *Lipaphis erysimi* – *Erysimum erysimoides*, *Macrosiphoniella absinthii* – *Artemisia absinthium*, *Macrosiphoniella artemisiae* – *Artemisia vulgaris*, *Macrosiphoniella kaufmanni* – *Achillea millefolium*, *A. pontica*, *Macrosiphoniella millefolii* – *Achillea millefolium*, *A. nobilis*, *Macrosiphoniella pulvera* – *Artemisia maritima*, *Macrosiphoniella stageri* – *Centaurea stoebe*, *Macrosiphoniella tanacetaria* – *Tanacetum vulgare*, *Macrosiphoniella xeranthemi* – *Xeranthemum foetidum*, *Macrosiphum euphorbiae* – *Euphorbia cyparissias*, *Metopeurum fuscoviride* – *Tanacetum vulgare*, *Microlophium evansi* – *Urtica dioica*, *Microsiphum nudum* – *Achillea nobilis*, *Mirotarsus cyparissiae* – *Euphorbia cyparissias*, *Myzus auctus* – *Cerastium tomentosum*, *Myzus persicae* – *Papaver dubium*, *Urtica urens*, *Myzus ajugae* – *Ajuga reptans*, *Pezoskia major* – *Echinops sphaerocephalus*, *Phalangomyzus oblongus* – *Artemisia vulgaris*, *Protaphis carlinae* – *Carlina* sp., *Pseudobrevicoryne erysimi* – *Erysimum crepidifolium*, *E. dubium*, *Semiaphis danci* – *Daucus carota*, *Siphia maydis* – *Medicago falcata*, *Siphia* sp. – *Agropyrum repens*, *A. sp.*, *Sitobium* spp. – *Festuca nemoralis*, *Lolium* sp., *Dactylis glomerata*, etc., *Stargiella necopinata* – *Galium verum*, *Therioaphis* spp. – *Melilotus albus*, *Medicago sativa*, etc., *Titanosiphon artemisiae* – *Artemisia campestris*. Parasites: *Aphidius absinthii* – *Macrosiphoniella absinthii*, *M. artemisiae*, *M. kaufmanni*, *M. millefolii*, *M. pulvera*, *M. stageri*, *M. xeranthemi*, *Aphidius avenae* – *Sitobium* spp., *Aphidius ervi* – *Acyrtosiphon pisum*, *A. spartii*, *Microlophium evansi*, *Aphidius fovealis* – *Dactynotus aeneus*, *D. campanulae*, *D. pictidis*, *D. sonchii*, *Pezoskia major*, *Aphidius matricariae* – *Galiobium laugei*, *Hyadaphis hofmanni*, *Linosophon asperulophagus*, *Myzus ajugae*, *Aphidius mirotarsi* – *Mirotarsus cyparissiae*, *Aphidius pascuorum* – *Sitobium* sp., *Aphidius phalangomyzi* – *Phalangomyzus oblongus*, *Aphidius picipes* – *Myzus auctus*, *M. persicae*, *Aphidius salicis* – *Aphis laubersi*, *Cavariella* spp., *Semiaphis danci*, *Aphidius sonchii* – *Hyperomyzus lactucae*, *Aphidius tanacetarius* – *Metopeurum fuscoviride*, *Diaretia rapae* – *Brachycaudus helichrysi*, *B. rumexicoleus*, *Brevicoryne brassicae*, *Dactynotus* sp., *Hayhurstia atriplicis*, *Myzus persicae*, *Sitobium* sp., *Ephedrus campestris* – *Dactynotus aeneus*, *D. cichorii*, *D. jaceae*, *D. obscurus*, *D. pictidis*, *D. sonchii*, *Macrosiphoniella absinthii*, *M. millefolii*, *Ephedrus nacheri* – *Cryptosiphum artemisiae*, *Hayhurstia atriplicis*, *Ephedrus persicae* (rare) – *Aphis fabae*, *Brachycaudus helichrysi*, *B. lychnidis*, *Ephedrus plagiator* – *Acyrtosiphon spartii*, *Aphis crataegae*, *A. fabae*,

A. urticae, *Rhopalosiphum padi*, *Sitobium* spp., *Lipolexis gracilis* – *Aphis cracciae*, *A. craccivora*, *A. euphorbiae*, *A. fabae*, *A. intybi*, *A. plantaginis*, *A. salviae*, *A. taraxacicola*, *Brachycaudus cardui*, *B. helichrysi*, *B. mordwilkoii*, *Lysaphidus arvensis* – *Coloradoa achilleae*, *C. artemisiae*, *C. tanacetaria*, *Lysaphidus erysimi* – *Lipaphis erysimi*, *Pseudobrevicoryne erysimi*, *Lysiphlebus ambiguus* – *Aphis urticae*, *Hyadaphis* sp., *Lysiphlebus arvicola* – *Siphia maydis*, *Siphia* spp., *Lysiphlebus fabarum* – *Aphis craccivora*, *A. euphorbiae*, *A. fabae*, *A. intybi*, *A. lambersi*, *A. newtoni*, *A. plantaginis*, *A. polygonata*, *A. pum.*, *A. poterii*, *A. roepkei*, *A. ruminis*, *A. salviae*, *A. stachydis*, *A. taraxacicola*, *A. thomasi*, *A. urticae*, *A. vanderghooii*, *A. verbasci*, *Brachycaudus cardui*, *B. rumicicolens*, *B. tragopogonis*, *Hyperomyzus lactucae*, *Microsiphium undum*, *Paczoskia major*, *Protaphis carlinae*, *Sitobium* sp., *Lysiphlebus fruticuliculi* – *Aphis cracciae*, *Lysiphlebus lurticornis* – *Metopeurum fuscoviride*, *Lysiphlebus melandriicola* – *Brachycaudus lychmidis*, *Paralipsis enervis* – *Anoecia* spp., *Aphis roepkei*, *Brachycaudus hallotae*, *B. cardui*, *B. mordwilkoii*, *Dysaphis crataegi*, *Praon absinthii* – *Macrosiphoniella absinthii*, *M. millefolii*, *Titanosiphon artemisiae*, *Praon dorsale* – *Acyrtosiphon pisum*, *Dactynotus campanulae*, *D. cichorii*, *D. jaceae*, *D. linariae*, *D. taraxacicola*, *Paczoskia major*, *Praon exoletum* – *Therioaphis* spp., *Praon volucre* – *Brachycaudus helichrysi*, *B. lychmidis*, *Brevicoryne brassicae*, *Hyperomyzus lactucae*, *Macrosiphium euphorbiae*, *Microlophium evansi*, *Sitobium* sp., *Trioxys angelicae* (rarely) – *Aphis fabae*, *Myzus persicae*, *Aphis salviae*, *Brachycaudus* sp., *Trioxys brevicornis* – *Cavaciella* sp., *Hyadaphis* sp., *H. bupleuri*, *Staegeriella necopinata*, *Trioxys centaureae* – *Dactynotus aeneus*, *D. campanulae*, *D. cichorii*, *D. jaceae*, *D. obscurus*, *Macrosiphoniella artemisiae*, *M. millefolii*, *M. tanacetaria*, *Microlophium evansi*, *Trioxys glaber* – *Aphis galii-scabri*, *Trioxys pannonicus* – *Titanosiphon artemisiae*, *Trioxys parvulus* – *Hyadaphis* sp. Fauna of meadows includes a great number of aphid and parasite species. Generally, and this generalization may well be documented by the above lists, it is a mixture of pest aphids, alternative hosts of useful parasites and indifferent species; both temporary and chronic sources of aphids may be found in meadows. The fauna of parasites includes both economically useful and indifferent species; the parasite foci are mostly of the chronic type. Due to the rather heterogeneous character of meadows, which cover also roadsides, orchard undergrowths, verges, etc., it seems that the pest aphids present here are usually very heavily influenced by the parasites: meadows are a perennial community, where the parasites find enough various hosts and successfully overwinter as well. Meadows—districts such as roadsides, verges, etc.—are well known foci, from which the parasites disperse to the neighbouring crop fields.

– *Reed thickets (Phragmites communis)*. Aphids: *Hyalopterus pruni*. Parasites: *Ephedrus plagiator*, *Praon volucre*, *Aphidius transcaspicus*—initial establishment. Reeds represent a perennial community, associated with ponds, marshes and wet meadows. They are often mixed with forest-type habitats. They are temporarily inhabited by *Hyalopterus pruni*, having *Prunus* spp. as its primary host plant. However, the primary and secondary host plants can often be found in the neighbourhood so that their habitat may be classified as identical. Chronic foci of parasites are included in forest habitats, from which the parasites disperse to reeds. Although reeds are a perennial community, they are infested by aphids only for a certain part of the season. Due to the life-cycle of the aphid and occurrence of chronic foci of parasites, reeds have connections with shrubs, deciduous forest edges, orchards, and gardens.

– *Ruderals*. Ruderal places, being associated with various plants, exhibit an extremely rich fauna of aphids and parasites. The aphids include pests, alternative hosts of useful parasites, and indifferent species. The composition of the ruderal flora may be either rather heterogeneous, or often a monoculture or several dominant species are found in a ruderal. Both annual and perennial plant species can be found here.

Achillea, *Artemisia*, *Tanacetum* are very common. They are infested by a spe-

cialized aphid fauna (*Macrosiphoniella*, *Dactynotus*, *Coloradoa*, *Metopennum*, etc.), to which a rather specialized complex of parasites is attached (*Aphidius*, *Ephedrus*, *Praon*, *Trioxys*). All of them represent almost entirely indifferent species.

Urtica dioica is mostly attacked by *Microlophium evansi* and *Aphis urticae*. Both aphids are entirely economically indifferent, but they are alternative hosts of a number of useful parasites.

Chenopodium and *Atriplex* are hosts of pest aphids such as *Aphis fabae* or *Myzus persicae* and aphids-alternative hosts of useful parasites (*Hayhurstia atriplicis*). Both pest aphids are attacked here by the same parasites as on various crops.

Cirsium—and *Carduus*—plants are mostly hosts of pest aphids: *Aphis fabae*, *Brachycaudus* spp., etc. Both these aphids occur here only seasonally, being dioecious species. The parasite complex is the same as in the crop fields.

The above mentioned examples illustrate the heterogeneity of relations of ruderals to other habitats as well as the necessity of individual approach to each weed plant. Data on aphids and parasites may be found in the above chapter (meadows).

The foci of parasites in ruderals are temporary or chronic, this depending on the species of the parasite.

— *Alfalfa field*. Aphids: *Acyrtosiphon pisum*, *Therioaphis* sp., *Aphis craccivora*. Parasites: *Aphidius ervi* — *Acyrtosiphon pisum*, *Praon exoleum* — *Therioaphis* sp., *Lipolexis gracilis* and *Lysiphlebus fabarum* — *Aphis craccivora*.

Alfalfa field is a perennial community. *Acyrtosiphon pisum* and *Therioaphis* sp. are monoecious species; alfalfa field includes their chronic sources, from which they disperse to other crops (*Acyrtosiphon pisum* to pea, clover, etc.) or to waste places, roadsides, etc. *Aphis craccivora* is probably a dioecious species, occurring on alfalfa in spring and in autumn only, being absent during the summer. Foci of parasites are also chronic. In *A. craccivora*, however, their character is more temporary; the parasites, due to the presence of their host, occur in the field in spring and in autumn only, they may overwinter here and reappear in spring, however, later in the season they are forced to disperse to the neighbourhood due to the seasonal absence of their host and lack of other suitable hosts in the alfalfa community. Alfalfa field, due to its perennial character and presence of chronic sources of aphids and foci of parasites, has close relations to the neighbourhood. *Acyrtosiphon pisum* attacks a number of leguminous plants, both crop and wild species, dispersing from alfalfa to annual leguminose crops namely. *Therioaphis* is a similar case. *Aphis craccivora* is widely eurytopic and polyphagous, occurring on a number of wild plants and causing damage to various crops.

— *Cereal crop field*. Aphids: *Anoecia* spp., *Metopolophium dirhodum*, *Rhopalosiphum padi*, *Sipha maydis*, *Sitobium* spp. Parasites: *Aphidius avenae* — *Sitobium* spp., *Ephedrus plagiator* — *Sitobium* spp., *Rhopalosiphum padi*, *Lysiphlebus arvicola* — *Sipha maydis*, *Paralipsis nervis* — *Anoecia* sp. (roots). Cereals are typical annual crops. The aphids can be divided into two groups: the first group includes the dioecious species such as *Rhopalosiphum padi* and *Anoecia* spp., which migrate to cereals from their primary host plants from forest type habitats; these aphids have mostly different parasites on their primary host plants (forest habitats) and on cereals (fields). The second group of aphids includes the monoecious species which live on various wild grasses and disperse to cereals during the season. As to the aphid biology, there are basic relations of cereals to the deciduous trees (forest type habitats and intermediate habitats) and to wild grasses (steppe type habitats). With respect to the parasites, there are relations to steppe habitats only (waste places, fallow lands, roadsides, etc.), while the penetration of some forest elements into cereal fields is still unclear.

— *Rape field*. Aphids: *Brevicoryne brassicae*. Parasite: *Diaretella rapae*. Rape is an

annual crop. *B. brassicae* disperses to the field from its hibernating sites, its sources in the field being temporary, similarly as with the foci of parasites. A rape field has close relations to cabbage fields and waste places namely, chronic foci of parasites may be found especially in waste places in spring, non-cultivated cabbage fields may serve as temporary foci of parasites as well.

— *Cabbage field.* Aphids: *Brevicoryne brassicae*, *Myzus persicae*. Parasites: *Diaeretiella rapae*. Cabbage is an annual or biennial crop, foci are temporary, similarly as with the sources of aphids, however, if there is no tillage in the autumn the parasites may hibernate in the field too. Sources of aphids and foci of parasites are almost identical, except that the foci of the parasites are more extensive due to their host specificity range. A cabbage field has close relations to other Brassicaceous crops and waste places, on which various brassicaceous weeds may also be found.

— *Potato field.* Aphids: *Aphis frangulae*, *Myzus persicae*, *Macrosiphum euphorbiae*, etc., Parasites: *Aphidius picipes* and *Diaeretiella rapae*—*Myzus persicae*. Potato is an annual community. All the aphids are seasonal pests, migrating to potatoes from the sources in the neighbourhood. Temporary foci of parasites are present in potato fields: *Aphidius picipes* seems to be attached to *Myzus persicae* exclusively, while *Diaeretiella rapae* parasitizes also *Brevicoryne brassicae* and *Hayhurstia atriplicis* that occur on various weed plants. Due to the life-cycle of aphids there are complicated relations between potatoes and other habitats where primary host plants and other sources of aphids occur. Parasites disperse to the field from chronic and temporary foci in the neighbourhood, apparently mostly from ruderals, fallow lands, and roadsides, but possibly from sugar beet fields, cabbage and rape fields in addition.

— *Sugar beet field.* Aphids: *Aphis fabae*, *Myzus persicae*. Parasites: *Lysiphlebus fabarum*, *Lipolexis gracilis*, *Trioxys aequalphae*—*Aphis fabae*, *Diaeretiella rapae*—*Myzus persicae*. Sugar beet is a typical annual crop, biennial if grown for seed. Both aphids mentioned occur here in spring—summer period, leaving the crop before harvest. Foci of parasites are extremely temporary, sometimes lasting a little longer due to the presence of weeds such as *Chenopodium*, on which both aphids feed and are also attacked by the same parasites as in the sugar beet. On some weeds (*Chenopodium*) some alternative hosts of the parasites can be found as well (*Hayhurstia atriplicis*—*Diaeretiella rapae*). Due to the life-cycle of aphids, sugar beet has close relations to the forest edges, etc., where primary host plants of pest aphids (*Aphis fabae*) occur. Sugar beet, too, is a source from which the aphids disperse to other crops and weeds during the season. As only temporary foci of parasites occur in the sugar beet field, the presence of chronic foci of parasites in the neighbourhood is important.

— *Classification.* In C. Europe, where a great part of the landscape represents cultivated areas, the research and classification of parasite foci is rather important.

In forests, which represent rather stable communities, mostly a good equilibrium is maintained except for some cases which are clearly a case of parasite inability to limit the host outbreak. A special problem is represented by aphids which are temporary inhabitants of forest-type habitats as they occur here on their primary host plants only, and migrate then to field crops causing damage there.

Orchards represent a great problem with respect to the presence or absence of foci in orchards or in their neighbourhood. Peculiarities of aphid life-cycle play a rather important role.

Meadows seem to be one of the habitats to which the biological control activities should be directed with respect to parasite conservation, as meadows include rather valuable chronic foci of various parasites. The heterogeneous character of plant composition and its aphidofauna are rather useful for various parasite species.

Meadow-type habitats are rather important for parasite conservation and their possible dispersal to field crops.

Perennial crops (alfalfa) seem to be rather useful with respect to biological control through the occurrence of chronic foci of parasites. The relatively stable environment allows us to classify the role of parasites in such environments with respect to natural limitation and aphid control.

Annual crops, being unstable environments, seem to represent rather difficult areas as to aphid control due to the dispersal and foci of parasites for example. The extensive acreage of a monoculture and relatively few places in the neighbourhood (chronic foci of parasites) from which the parasites would disperse to the crop in connection with dispersal of aphids, may be mentioned.

Ruderals. The position of ruderals must be classified with respect to separate cases and prevailing plant composition. On the one hand, they represent sources of pest aphids, on the other hand the chronic foci of parasites are also present. In certain cases they might be useful in biological control (conservation of parasites).

— SOUTH EUROPE (ITALY).

— *Sea-shore, grassy habitats and Macchia.* A comparatively narrow zone is formed by steppe type growth and fallow lands and various waste places not overgrown by trees belong to it as well.

Aphids: *Aphis* spp. — *Psoralea bituminosa*, *Sedum rupestre*, *Melilotus albus*, *Ranunculus bulbosus*, *Mentha arvensis*, *Brachycaudus* sp. — *Carduus pycnocephalus*, *Dactynotus* sp., — *Sonchus oleraceus*, *Hyperomyzus* sp. — *Sonchus oleraceus*, *Protophila* sp. — *Centaurea aspera*, *Siphia* sp. — *Lolium perenne* v. *rigidum*, *Hordeum murinum*, *Avena sativa* var. *barbata*, *Sitobium* sp. — *Avena sativa* var. *barbata*, Parasites: *Lysiphlebus arvicola* — *Siphia* spp., *Lysiphlebus ambiguus* and *L. fabarum* — *Aphis* spp., *Aphidius fumebris* — *Dactynotus* sp., *Trioxys aculephae* — *Aphis* spp., *Aphidius arenae* — *Sitobium* spp. A typical characteristic of this association is its seasonal occurrence, as due to the insolation the plants are mostly infested by a seasonal aphidofauna and there are, with some exception (*Lysiphlebus arvicola*) only temporary foci of parasites. *Siphia* species may be mentioned as a possible pest on cereals. It is a holocyclic species and it occurs in such and similar habitats all through the year, attacking various grasses; as its parasite, *L. arvicola*, is a strictly specialized species, the habitat includes its chronic foci. Therefore, grassy habitats on the sea-shore mostly include temporary foci of parasites, with the exception of *L. arvicola* that occurs here perennially in chronic foci. In the close vicinity of this zone there are shrubs and trees, among which are often situated orchards (olives, fruit trees) or small oat fields, carnation fields, and small places of more or less natural community, the macchia forest. In olive and fruit orchards there is a comparatively specifically numerous undergrowth of various herbs that represent a natural intermediary zone between the steppe coastal zone and shrubs and trees. Aphids: On trees and shrubs — *Aphis pomi* — *Crataegus* sp., *Malus silvestris*, *Aphis* spp. — *Tamarix* sp., *Rubus* spp., *Sarothamnus scoparius*, *Cnara* sp. — *Pinus halepensis*, *P. maritima*, *Forda* spp. — *Pistacia terebinthus*, *P. lentiscus*, *Hyalopteris pruni* — *Prunus persica*, *Hyadaphis* sp. — *Lonicera implexa*, *Myzus varians* — *Prunus persica*, *Schizoneura* sp. — *Ulmus campestris*. The grassy undergrowth and open places — *Aphis fabae* — *Fumaria capreolata*, *Vicia sativa* var. *macrocarpa*, *V. faba*, *Aphis thloris* — *Hypericum perforatum*, *Aphis* sp. — *Torilis arvensis*, *Centranthus ruber*, *Lavatera cretica*, *Pittosporum tobira*, *Sedum rupestre*, *Rubia tinctorum*, *Carduus pycnocephalus*, *Euphorbia cyparissias*, *Anuni majus*, *Chrysanthemum segetum*, etc., *Aulacorthum* sp. — *Pelargonium* sp. (ornamental), *Brevicoryne brassicae* — *Moricandia arvensis*, *Dactynotus* spp. — *Sonchus arvensis*, *S. oleraceus*, *Reichardia pictoides*, *Longiunguis donacis* — *Arundo donax*, *Macrosiphum rosae* — *Rosa* sp., *Schiz-*

aphis longicauda - *Arundo donax*. Parasites: *Aphidius fovealis* - *Dactynotus* spp., *Aphidius rosae* - *Macrosiphum rosae*, *Aphidius transcaspicus* - *Hyalopterus pruni*, *Longinotus donatus*, *Ephedrus plagiator* - *Aphis* spp., *Lysiphlebus ambiguus*, *Monoctonia pistaciaecola* - *Forda* spp., *Panisia* sp. - *Cuscuta* spp., *Praon volucre* - *Hyalopterus pruni*, *Trioxys aculephae* - *Aphis* spp., *Trioxys angelicae* - *Aphis pomi*. The community represents a highly mixed complex. The forest and steppe habitats are mixed with various cultivated plots. For this reason, in many cases chronic foci of parasites can be found here. Pest aphids—*Aphis pomi*, *Hyalopterus pruni*, *Aphis fabae*—find various host plants among the cultivated and wild species, the habitat including therefore their perennial sources. Of the useful parasites, the following species can be mentioned: *Aphidius transcaspicus*, *Ephedrus plagiator*, *Lysiphlebus ambiguus*, *Praon volucre*, *Trioxys aculephae*, *T. angelicae*. Therefore, a semicultivated macchia forest includes chronic foci of parasites. Both pest species and alternative hosts of useful parasites are present.

- *Orchards*. Various orchards, mainly citrus, peach and mixed orchards were studied. The undergrowth is very heterogeneous and depends on the degree of cultivation. Aphids: Orchard trees - *Aphis pomi* - *Malus silvestris*, *Cydonia* sp., *Aphis punicae* - *Punica granatum*, *Aphis* spp. - *Liquiritia* sp., *Nespilus germanica*, *Brachycaudus* sp. - *Prunus persica*, *P. amygdalus*, *Chromaphis juglandicola* - *Juglans regia*, *Hyalopterus pruni* - *Prunus persica*, *Myzus* sp. - *Prunus persica*, *Toxoptera aurantii* - *Citrus* sp. Undergrowth - *Acyrtosiphon pisum* - *Melilotus albus*, *Aphis fabae* - *Chenopodium* sp., *Aphis umbrellae* - *Malva silvestris*, *Aphis* spp. - *Papaver rhoeas*, *Amaranthus ascendens*, *Polygonum lapathifolium*, *Rubus* sp., *Melilotus albus*, *Urtica urens*, *Brachycaudus* sp. - *Carduus pycnocephalus*, *Brevicoryne brassicae* - *Erysimum hieracifolium*, *Dactynotus* sp. - *Sonchus oleraceus*, *Inula viscosa*, *Carthamus lanatus*, *Hayhurstia atriplicis* - *Chenopodium* sp., *Hyperomyzus* sp. - *Sonchus oleraceus*, *Macrosiphoniella* sp. - *Artemisia* sp., *Semiaphis dauci* - *Daucus carota*, *Siphia* sp. - *Avena sativa*, *Sitobion* sp. - *Avena sativa*. Parasites: *Aphidius absinthii* - *Macrosiphoniella* sp., *Aphidius fovealis* - *Dactynotus* sp., *Aphidius transcaspicus* - *Hyalopterus pruni*, *Aphidius eri* - *Acyrtosiphon pisum*, *Diaretella rapae* - *Brevicoryne brassicae*, *Lipolexis gracilis* - *Aphis* spp., *Toxoptera aurantii*, *Lysiphlebus ambiguus* - *Aphis* spp., *Praon volucre* - *Hyalopterus pruni*, *Trioxys angelicae* - *Aphis* spp., *Toxoptera aurantii*.

ways. Irrigating ditches and their neighbourhood are bordered by *Populus* sp. (*Chaitophorus* sp., *Pterocomma* spp.) and often grown by *Arundo donax* (*Longiunguis donacis*) and *Phragmites communis* (*Hyalopterus pruni*). An orchard neighbourhood is extremely important with respect to foci of parasites of orchard pest aphids and sources of aphid pests. In this respect, *Pittosporum tobira*, *Crataegus* and *Glyphinia*, *Phragmites* may be said to be unsuitable as they represent sources of pest aphids that infest fruit trees in orchards. On the contrary, the occurrence of *Nerium oleander*, *Hedera helix*, *Rosmarinus officinalis*, *Arundo donax* in hedges seems to be beneficial as their aphid fauna is economically indifferent and represents alternative hosts of orchard pests. Some other plants, such as *Quercus*, *Rosa* and *Populus* are quite indifferent to the orchards. Orchards themselves have certain relations to related types of forests and parks: the undergrowth has relations to steppe, fields, meadows and ruderals.

- *Alfalfa field*. Aphids: *Acyrtosiphon pisum*, *Therioaphis trifolii*. Parasites: *Aphidius ervi* and *Praon dorsale* - *Acyrtosiphon pisum*, *Praon exoletum* - *Therioaphis trifolii*. Alfalfa field is a perennial community. It includes chronic foci of parasites of both aphids mentioned.

Due to the presence of chronic sources of aphids and chronic foci of parasites, the alfalfa field is a source from which the aphids and parasites disperse to the neighbourhood—to annual crops, etc. In meadows, waste places, etc., there can be plants (Leguminous) infested perennially by the same aphids and parasites—chronic sources and foci occur here as well.

- *Afforestation belts, sea-shore*. In afforestation of sea-shore sands in S. Italy (Sicily) *Eucalyptus* tree and *Pinus pineopinaster* are used. Aphids: *Cinara* sp. - *Pinus pineopinaster*. *Eucalyptus* - no aphids. Parasites: *Panesia* sp. - *Cinara* sp. Afforestation groves represent forest-like associations where chronic foci of *Cinara* parasites can be found. The *Eucalyptus* tree is indifferent. However, there are no relations to other habitats, the aphids associated with *Pinus* and their parasites being connected with conifers exclusively. There are no relations to cultivated crops either. There may be certain affinities to the macchia forest (coniferous trees as well).

- *Valleys of rivers*. Aphids: *Aphis nerii* - *Nerium oleander*, *Aphis* sp. - *Tamarix* sp., *Chaitophorus* sp. - *Populus* sp., *Dactynotus inulae* - *Inula viscosa*, *Longiunguis donacis* - *Arundo donax*, *Pemphigus* sp. - *Populus* sp., *Sipha* sp. - *Agropyrum* sp., *Hyalopterus pruni* - *Phragmites communis*. Parasites: *Aphidius transcaspicus* - *Hyalopterus pruni*, *Longiunguis donacis*, *Lysiphlebus arvicola* - *Sipha* sp., *Lysiphlebus salicaphis* - *Chaitophorus* sp., *Monoclonia pistaciaecola* - *Pemphigus* sp., *Ephedrus campestris* - *Dactynotus inulae*, *Praon volucre* - *Hyalopterus pruni*.

Valleys of rivers and brooks represent a mixture of various elements: Elements of deciduous forests following the rivers, besides, there are numerous weeds and other plants of the neighbouring habitats represented in such communities. Due to the partially evergreen character of associated communities, chronic and temporary foci of parasites are present; they may include both useful and indifferent species. Sources of water—the rivers, brooks and irrigating ditches—are extremely important for agriculture because of irrigation, microclimate conditions, etc. The water sources are, therefore, connected with all the various habitats from forest to semidesert landscapes, they are transzonal. The high humidity near the rivers and brooks enables the existence of forest elements and associated aphid fauna far to the south, the neighbourhood being different. As a result, valleys of rivers represent habitats from which, on the one hand, the forest fauna disperses into suitable neighbouring habitats, on the other hand, a number of steppe and semidesert species are concentrated here during the hot summer period. These features give the river valleys, brooks and

irrigating ditches great importance. Besides indifferent species (*Ephedrus campestris*), many useful species are present here which attack certain aphid species, but may disperse to suitable habitats in the neighbourhood: *Trioxys angelicae* parasitizes *Aphis* spp. here, but attacks *Toxoptera aurantii* in the Citrus groves. *Lysiphlebus ambiguus*, a common parasite of *Aphis farinosa* on *Salix*, is a similar case. In other cases, there may be also sources of pest aphids and foci of associated parasites. Example: *Hyalopterius pruni* on *Phragmites communis*. It disperses from here to peach orchards. Its parasite, whose chronic foci are in reeds, attacks both *Hyalopterius pruni* on *Phragmites* and *Longiunguis donacis* on *Arundo donax*. If the fact that *Phragmites communis* and *Arundo* reeds are associated with irrigating ditches near peach orchards is taken into consideration, the importance of the habitat relationship is apparent.

- *Classification*. In the arid districts of S. Italy the most important seem to be the river and brook valleys, irrigating ditches, and all the moist habitats, where chronic foci of parasites and often chronic sources of pest aphids may be found. The remains of virgin steppe, semidesert, waste land, etc., seem to have a minor importance due to their seasonal character which mostly allows the presence of temporary foci of parasites only.

- CAUCASUS (GEORGIA).

- *Citrus and tea plantations*. The Black Sea Coast district is a part of the Mediterranean Citrus growing area. Citrus and tea plantation are mixed; sometimes tea is grown as a shrub layer of Citrus orchards. Besides other orchards, parks and gardens are common, as well as shrubs, fallow land and small forests. Aphids: *Toxoptera aurantii* - Citrus spp., *Thea sinensis*, *Camelia* sp. (ornamentals), *Aphis craccivora* - Citrus sp. Parasites: *Lysiphlebus ambiguus* - *Toxoptera aurantii*, *Aphis craccivora*, *Aphis* spp. (undergrowth), *Lipolexis gracilis* - *Toxoptera aurantii*, probably also *Trioxys angelicae*. As to its origin, *Toxoptera aurantii* is an introduced pest, while its parasites on the Black Sea Coast are indigenous. Because of seasonal outbreaks of the pest, it is apparent that the parasites are not capable of limiting the pest throughout the season. The community of Citrus plantations is evergreen. Chronic foci of parasites are both in orchards and plantations as well as in other evergreen or deciduous communities. Parasites of Citrus and tea pests occur in the neighbourhood of orchards as well, while *Toxoptera aurantii* seems to be restricted to Citrus and tea associations exclusively.

- *Classification*. Considering the Black Sea Coast zone and evergreen character of many of its communities we can classify this zone as possibly rather useful for biological control. Introduced parasites are recommended to belong to parasites of aphidine aphids, both climate and presumed alternative hosts, besides *Toxoptera aurantii*, the control object, seem to be suitable.

- CENTRAL ASIA (USSR).

- *Virgin semidesert*. The virgin salt semidesert studied was characterized by scattered growth of various salsolaceous plants. On them, *Aphis craccivora* was the most common, besides other typical species associated with *Tamarix*, etc. *Lysiphlebus ambiguus* was the only parasite ascertained here. Due to the biology of the aphid, its occurrence on various salsolaceous plants can be classified as temporary. Rich plant communities were associated with small rivers in the semidesert. There *Populus* and *Salix* were rather common, together with many other plants. *Aphis farinosa* is common on willows, parasitized by *Lysiphlebus ambiguus*. Chronic foci of the parasite are probably situated in similar habitats in the virgin semidesert landscape. In connection with the cotton field, etc., it is necessary to stress the fact that willows and poplars are commonly grown along irrigating ditches as well.

- Cotton field. Aphids: *Aphis craccivora*, *A. gossypii* and *Acyrtosiphon gossypii* seem to be the main aphid pests on cotton in C. Asia. Parasites: *Lysiphlebus ambiguus* - *Aphis* spp., *Praon dorsale* and *Trioxys asiaticus* - *Acyrtosiphon gossypii*. Cotton, not being a perennial crop, is attacked by aphids during a part of the season only, in a similar way to other plants. The life-history of the aphids and their sources are different: *Medicago sativa*, the alfalfa, is the main host of *Aphis craccivora*, on which it overwinters, reproduces in spring and disperses to *Robinia pseudoacacia*, cotton and various leguminous plants. Alfalfa fields, therefore, include sources of the aphid, the occurrence, however, of the aphid here is temporary. During summer, aphids occur mostly in irrigated areas, on desert wild plants (*Althagi camelorum*), remigrating to alfalfa in the autumn. Alfalfa, *Robinia pseudoacacia* and wild leguminous plants represent thus the main sources of the pest. There are various opinions as to the role of *Robinia*. Some authors classify it as a source, others as a plant which attracts the aphids from cotton, leguminous plants both wild and cultivated being the major sources. According to DAVLETSHINA (1956, etc.) the infestation of cotton is due to the migration of aphids to different plants, be they primary or secondary hosts. Therefore, both alfalfa fields, *Robinia* growths and wild plants represent sources of the cotton aphid pest.

Acyrtosiphon gossypii occurs on various Leguminosae. Its main sources, the typical semidesert plants such as *Althagi camelorum*, and others, are its primary sources from which it disperses to cotton.

Aphis gossypii is a widely polyphagous species, occurring on a number of wild and cultivated plants. It hibernates in adult stage on various weeds, which are also its sources in spring; later in the season they attack cotton and other crops, being concentrated during summer on various cultivated crops (Cucurbitaceae) and returning to various wild plants in and near cotton fields in autumn. Again, wild habitats contain the main sources of pest aphids. The occurrence and relations of wild and cultivated crops have been well observed and documented by many authors (see: DAVLETSHINA, 1956). Parasites attack the aphids both in wild and cultivated habitats, yet their foci in the fields seem to be temporary. Wild habitats represent thus the main sources and reservoirs of the cotton pest aphids, alfalfa fields being also important; from them, the pest aphids disperse and attack the cotton. Parasites occur in the same habitats as the aphids, their chronic foci being in wild and non-cultivated land, cultivated land including temporary foci only.

- Alfalfa field. Aphids: *Acyrtosiphon pisum*, *Therioaphis* sp. (*Aphis craccivora* not found by us). Parasites: *Aphidius ervi*, *Praon dorsale* - *Acyrtosiphon pisum*, *Praon exoletum*, *Trioxys complanatus* - *Therioaphis* sp.

Alfalfa field is a perennial community, it includes chronic sources of aphids and chronic foci of parasites. Both aphids mentioned are pests. The same *Therioaphis* sp. was found on *Melilotus officinalis* at a neighbouring semidesert place, being attacked by *Praon exoletum* (and probably by *Trioxys complanatus* in addition). This means that chronic sources of pests and chronic foci of parasites occur in the neighbourhood of the field as well, *Acyrtosiphon pisum* is a similar case. Moreover, *Praon dorsale* attacks also various Dactynotine aphids, which are associated with various semidesert plants and weeds, as well as *Acyrtosiphon gossypii* which is also a pest on cotton.

- Oases. Because of irrigation and the intensive agricultural activities of man, oases exhibit a rather numerous and heterogeneous fauna of aphids and parasites. Many species are connected with shady and ornamental trees, others are pests of agricultural crops on irrigated land; others still are associated with weeds or original semidesert habitats, which either occur on semidesert plots in the cultivated landscape, or which adapted themselves to the new type of landscape. All these elements are distributed

to a various degree in various habitats in the irrigated land of oases. Annual, biennial, and perennial crops have various relations as to the aphids and parasites. We have only touched on this rather extensive problem, dealing with the relations of *Populus*, *Salix* and *Robinia* grown near and along irrigation ditches. Poplars are mainly attacked by various *Chaitophorus* sp., which are parasitized by a specialized parasite *Lysiphlebus salicaphis*, this means that the aphid and parasite fauna of poplars has no relation to the crops in the neighbourhood. *Salix* trees, being attacked by a number of aphids exhibit other features: Besides *Chaitophorus* sp. they are commonly attacked by *Aphis farinosa*, which is one of the main hosts of *Lysiphlebus ambiguus*. *Robinia pseudoacacia*, a leguminous tree, is a common temporary host of *Aphis craccivora*. Here, also, the aphid is attacked by *Lysiphlebus ambiguus*. The relationship among the aphids and parasites and their dispersal in the neighbourhood is very important. *Lysiphlebus ambiguus* attacks both *Aphis farinosa* and *A. craccivora* at the same habitat—in its chronic foci—so that a lower number of *A. craccivora* can disperse to cotton. Further, *L. ambiguus* is capable, though originally a forest inhabitant, to disperse and occur in the neighbouring areas such as cotton fields, etc., as well. These features show, on the one hand, the significance of parasite foci with regard to the pest aphids and their limitation, on the other hand, the unsuitability of *Robinia* due to its being a temporary host of the cotton pest aphid. However, as *Robinia* is a valuable honey plant, we must expect it will be grown again in the habitats mentioned, so that only its coexistence with *Salix* or its presence in the neighbourhood might be projected to put *Aphis craccivora* at least under the influence of chronic foci of its parasite.

—*Classification.* It was shown above that there are mostly only temporary foci of parasites present in cultivated crops, the exception being alfalfa, while chronic foci are in some kinds of the neighbouring environments. Neighbourhoods of irrigated ditches, river banks, all these habitats include chronic foci of parasites as well as intensively irrigated gardens and parks.

—CUBA.

—*Tropical cloud forest.* Example: Pico de Cuba, Pico Turquino, Sra. Maestra

Aphids: *Acyrtosiphon bidenticola* — *Bidens pilosa*; *Aphis spiraeicola* — *Rubus turquinensis*, *Lisianthus glandulosus*, *Eulophia alta*, *Eupatorium* spp., *Bidens pilosa*; *Aulacorthum solani* — *Rubus turquinensis*, *Bocconia frutescens*, *Gnaphalium americanum*, *Crepis japonica*, *Fragaria* sp.; *Brachycaudus helichrysi* — *Gnaphalium americanum*, *Erechthites* sp.; *Dactynotus ambrosiae* — *Sonchus oleraceus*; *D. sp.* — *Gnaphalium americanum*, *Vaccinium leonis*; *Hyperomyzus lactucae* — *Sonchus oleraceus*; *Hystero-neura* sp. — *Granuncac.* *Neolizerius* sp. — *Nectandra reticularia*; *Neomyzus circumflexus* — *Rubus turquinensis*, *Vaccinium leonis*, *Fragaria* sp., *Rhopalosiphum latysiphon* — *Fragaria* sp.; *Rhopalosiphum* sp. — *Gramineae*. *Sitobium luteum* — *Eulophia* sp., *Epidendrum crassilabium*, *Lepanthes licheniana*, *Epidendrum teretifolium*; *Toxoptera auranti* — ferns, *Micania cordifolia*, *Cleyera* sp., *Vaccinium leonis*, *Ilex Macfaydeni*, *Stelix ophioglossoides*, *Buchenavia* sp., *Tortallasia cuneifolia*, *Salvia nigrescens*, *Eupatorium* sp. Parasites: *Ephedrus incompletus* — *Aulacorthum solani*; *Lysiphlebus testaceipes* — *Aphis spiraeicola*, *Brachycaudus helichrysi*, *Rhopalosiphum latysiphon*, *Sitobium luteum*, *Toxoptera auranti*, *Pseudephedrus neotropicalis* — *Neolizerius* sp.; *Trioxys silvicola* — *Aulacorthum solani*, *Sitobium luteum*. Analysis: *Toxoptera auranti* and *Aphis spiraeicola* are indifferent here but they are pests on cultivated crops—the zone represents a possible source of pest aphids. Of the parasites, only *Lysiphlebus testaceipes* is a parasite of economically important aphids. The rest of aphids and parasites are economically indifferent species. Conclusions: Tropical cloud forest zone includes chronic foci of parasites, of these, *L. testaceipes* is valuable. The zone includes chronic sources of *Toxoptera auranti* and *Aphis spiraeicola* pest aphids; they do not cause

economic losses here due to the absence of cultivated crops. Relations to other habitats: Due to its occurrence and conditions in high mountains this zone is well separated from the influence of agriculture. Due to the existence of pathways, etc., a certain number of weed plants may be found here. There are close connections with another evergreen formation, the rain forest.

– *Tropical rain forest.* Example: Valley of river Yara, nr. Santo Domingo, Sra. Maestra range.

Aphids: *Aphis craccivora* – *Micania* sp., *Theobroma cacao*, *Gliricidia sepium*, *Citrus* sp., *Aphis coreopsidis* – *Bidens pilosa*; *Aphis gossypii* – *Colocasia antiquorum*, *Hibiscus rosa-sinensis*, *Tridax procumbens*, *Bidens pilosa*; *Aphis illinoensis* – *Vitis tiliacifolia*, *Cissus sicyoides*; *Aphis nerii* – *Asclepias curasavica*; *Aphis spiraeicola* – *Pothomorphe peltata*, *Tournefortia* sp., *Solanum antillarum*, *Viburnum villosum*, *Ageratum conyzoides*, *Theobroma cacao*, *Annona squamosa*, *Eupatorium macrophyllum*; *Brachycaudus helichrysi* – *Erechtithes hieracifolia*; *Dactynotus ambrosiae* – *Micania micrantha*, *Erechtithes hieracifolia*, *Sonchus oleraceus*; *Dactynotus erigeronensis* – *Erigeron canadensis*; *Hyperomyzus lactucae* – *Sonchus oleraceus*; *Hysteronentra* sp. – *Gramineae*; *Lipaphis erysimi* – *Brassica campestris*, *Macrosiphum mesosphaeri* – *Hyptis verticillata*; *Pentalonia nigronervosa* – *Musa paradisiaca*; *Sitobium salviae* – *Salvia miselia*, *Tetraneura hirsuta* – *Gramineae*; *Toxoptera aurantii* – *Coffea arabica*, *Theobroma cacao*, *Citrus* sp. Parasites: *Acanthocaudus tissoti* – *Dactynotus ambrosiae*; *Aphidius floridacensis* – *Dactynotus ambrosiae*, *D. erigeronensis*; *Diaeretiella rapae* – *Lipaphis erysimi*; *Ephedrus incompletus* – *Sitobium salviae*; *Lysiphlebus testaceipes* – *Aphis spiraeicola*, *A. nerii*, *A. coreopsidis*, *A. illinoensis*, *A. gossypii*, *Sitobium salviae*, *Dactynotus ambrosiae*, *D. erigeronensis*, *Brachycaudus helichrysi*; *Trioxys* sp. – *Macrosiphum mesosphaeri*. Analysis: *Aphis spiraeicola*, *A. gossypii*, *A. craccivora*, *Toxoptera aurantii*, pest aphids on cultivated crops in the lowlands, occur commonly in this zone. They also attack crops grown here: cocoa, coffee, citrus. *Lysiphlebus testaceipes* is the only significant parasite; the rest of the species is indifferent. Indifferent species of aphids are also present, some of them represent hosts of *L. testaceipes* as well.

Conclusions: Tropical rain forest zone includes chronic foci of parasites, *L. testaceipes* being the most valuable. Chronic sources of aphid pests are also present, the aphids being either economically indifferent or causing certain damage here. Relations to other habitats: Some districts of the forest are changed through deforestation, pastures, corn fields, banana plantations, etc., appearing in consequence. The roads and pathways in the forest are inhabited by typical weeds and associated aphid fauna. Generally, continuous sources of aphids can be found in the rain forest community, however, the aphids can find so many food sources in the community that their attack on crops (*Toxoptera aurantii*) does not seem to be of such a serious significance as in a savanna landscape.

– *Tropical deciduous forest.* Example: Belic, env. Niquero.

Aphids: *Aphis coreopsidis* – *Bidens pilosa*; *Aphis gossypii* – *Cecropia peltata*, *Sida rhombifolia*; *Aphis spiraeicola* – *Bursera simaruba*, *Eupatorium* sp.; *Rhopalosiphum maidis* – *Zea mays*; *Toxoptera aurantii* – *Cassia hirta*, *Krugiodendron ferreum*, *Calyptanthus chytaculia*, *Clusia rosca*, *Acrosynanthus latifolium*, *Coccoloba diversifolia*. Parasites: *Lysiphlebus testaceipes* – *Aphis coreopsidis*, *A. gossypii*, *A. spiraeicola*, *Rhopalosiphum maidis*, *Toxoptera aurantii*. Analysis: *Aphis gossypii*, *A. spiraeicola*, *Toxoptera aurantii* occur commonly in this zone, both on native and cultural (weeds, crops) elements. *Lysiphlebus testaceipes* is the only effective parasite present, some of the economically indifferent aphids being its hosts as well. Conclusions: Tropical deciduous forest zone includes chronic foci of parasites. In this zone, too, chronic sources of aphids are present.

- *Tropical dry forest*. Example: Tortuguilla, nr. Guantánamo.

Aphids: *Aphis craccivora* - *Tephrosia cinerea*, *Aloe* sp. Parasites: No parasites found; they apparently are very rare due also to the rare aphid colonies present. Analysis: This zone rarely includes foci of parasites, only occasionally. Conclusions: This zone is not suitable either for aphids or parasites. They can be found in neighbouring habitats—villages, roadsides, etc.—which represent the results of man's invasion. Relations to other habitats: Due to its character, it is strictly separated from other habitats.

Weeds and ruderal flora may penetrate into this zone following the roads.

- *Mangrove forest*. Example: Playa del Máquina, Peninsula de Zapata.

Aphids: *Aphis spiraeicola* - *Eupatorium*; *Dactynotus ambrosiae*. Parasites: *Lysiphlebus testaceipes* - *Aphis spiraeicola*. Analysis: The occurrence both of aphids and parasites is very rare. Foci of parasites seem to be temporary, apparently due to the dispersal from neighbouring habitats (tropical deciduous forest, etc.). Conclusions: This zone is not suitable either for aphids or parasites. Relations to other habitats: Due to their character, they are strictly separated from other habitats, nevertheless, intermediary zones may be found.

- *Savanna*. Example: Dayanguas, nr. San José, Pinar del Río prov.

Aphids: *Aphis spiraeicola* - *Solanum* sp. Parasites: No parasites found. Analysis: Virgin savanna does not seem to be suitable either for aphids or parasites. Foci of parasites apparently have a temporary character. Conclusions: This zone is not suitable either for aphids or parasites.

Example: Guanímar, Habana prov.

Aphids: *Aphis craccivora* - *Viciaeae*, *A. gossypii* - *Ruellia* sp., *Aphis spiraeicola* - *Calophyllum antillanum*; *Dactynotus ambrosiae* - *Pluchea* sp.; *Toxoptera aurantii* - *Calophyllum antillanum*. Parasites: *Lysiphlebus testaceipes* - *Toxoptera aurantii*. Analysis: In the virgin savanna the occurrence of aphids and parasites is rare, both groups may be more common on secondary elements; in the latter case, chronic foci of parasites may be present. Conclusions: Virgin savanna is not a suitable habitat either for aphids or parasites. Secondary changes (man's activity, growing crops, etc.) apparently cause corresponding changes in the fauna too.

- *Sea shore*. Example: Dayanguas, env. of San José, Pinar del Río prov.

Aphids: No aphids. Parasites: No parasites. Analysis: Halophytic locality with mangrove forest elements apparently is not suitable either for aphids or parasite occurrence (salinity). Conclusions: Virgin sea shore is not suitable for aphids and parasites.

Example: La Habana, env. of the town.

Aphids: *Aphis craccivora* - *Tribulus cristoides*; *Aphis coreopsidis* - *Bidens pilosa*; *Hyperomyzus lactucae* - *Sonchus oleraceus*. Parasites: *Lysiphlebus testaceipes*. Analysis: The occurrence both of aphids and parasites is apparently due to the presence of ruderal flora (weeds), temporary foci of parasites are present. Conclusions: Sea shore districts secondarily inhabited by ruderal flora include temporary foci of parasites. Pest aphids may also be present. Relations to other habitats: Virgin sea-shore is inhabited by rather specific flora with poor relations to other communities. Nevertheless, many other communities may spread to this zone.

- *Parks*. Example: La Habana

Aphids: *Aphis craccivora* - *Cassia* sp., *Gliricidia sepium*, *Pittosporum tobira*; *Aphis gossypii* - *Acalypha* sp., *Hibiscus rosa-sinensis*, *H. schizopetalus*; *Aphis spiraeicola* - *Annona* sp., *Araliaceae* sp., *Bursera sumatuba*, *Citrus* sp., *Calophyllum antillanum*, *Croton* sp., *Ixora coccinea*, *Ceraiaaphis* sp. - *Cocos nucifera*; *Penalonia nigronervosa* - *Musa* sp., *Alpinia* sp., *Rhodobium porosum* - *Rosa* sp., *Toxoptera aurantii* - *Annona*

sp., *Citrus* sp., *Calophyllum antillanum*, *Mangifera indica*. Parasites: *Lysiphlebus testaceipes*. Analysis: The community is artificial, being mostly composed of various introduced plants, nevertheless, it is an evergreen association due both to the composition of plants and irrigation. Chronic foci of parasites occur here. *Aphis craccivora*, *A. gossypii*, *A. spiraeicola* and *Toxoptera aurantii* occur commonly on various plants, there are chronic sources of these pests in the habitat. Chronic foci of parasites (*Lysiphlebus testaceipes*) are present as well. Conclusions: Evergreen character of the community and its wide distribution in cultivated areas (towns, villages) and the presence of chronic sources of aphids and foci of parasites make this type of habitat extremely important. Relations to other habitats: Parks have close relations to forests, orchards, way-side trees in many respects. Besides, ruderal and weed flora is common in undergrowth and on waste places.

- *Botanical gardens*. Example: Botanical garden, La Habana.

Aphids: *Aphis craccivora* - *Cassia fistula*; *Aphis coreopsidis* - *Bidens pilosa*; *Aphis gossypii* - *Gossypium* sp.; *Vinca minor*, *Hibiscus rosa-sinensis*, *Acalypha alopecuroides*, *Acalypha* sp.; *Aphis illinoensis* - *Vitis vinifera*; *Aphis nerii* - *Nerium oleander*, *Callotropis procera*; *Aphis spiraeicola* - *Polyscias guilfoylei*, *Cassia alata*, *Citrus* sp., *Bursera simaruba*, *Eupatorium* sp.; *Chaitophorus* sp. - *Salix* sp.; *Cinara tujaefolia* - *Thuja occidentalis*; *Hysteronura setariae* - Gramineae. *Myzus persicae* - *Brassica urbaniana*; *Pentalonia nigronervosa* - *Musa* sp., *Alpinia speciosa*, *Rhodobium porosum* - *Rosa* sp.; *Toxoptera aurantii* - *Terminalia catappa*, *Tectona grandis*, *Mangifera indica*, *Calophyllum antillanum*, *Citrus* sp., *Bursera simaruba*. Parasites: *Lysiphlebus testaceipes* - *Aphis craccivora*, *A. coreopsidis*, *A. gossypii*, *A. illinoensis*, *A. nerii*, *A. spiraeicola*, *Hyperomyzus lactucae*, *Hysteronura setariae*, *Pentalonia nigronervosa*, *Toxoptera aurantii*. Analysis: The community is artificial and it is composed of plants which are mostly of exotic origin. It is at least partly an evergreen association. Chronic foci of parasites are present, *Lysiphlebus testaceipes* being the important species; both pest and indifferent aphids fall within its host range. Of the aphids, *Aphis spiraeicola*, *Toxoptera aurantii*, *Myzus persicae*, *Hysteronura setariae*, *Aphis gossypii*, *A. craccivora* are pests on cultivated crops, while the rest includes economically indifferent species; due to their character, botanical gardens represent chronic sources of aphids. Conclusions: Botanical gardens include chronic foci of parasites as well as chronic sources of pest aphids. Relations to other habitats: They are principally similar as in parks.

- *Way-side trees, avenues*. Example: Various habitats all over Cuba.

Aphids: *Aphis craccivora* - *Gliricidia sepium*; *Aphis nerii* - *Nerium oleander*; *Aphis spiraeicola* - *Bursera simaruba*; *Toxoptera aurantii* - *Calophyllum antillanum*. Parasites: *Lysiphlebus testaceipes*. Analysis: Both chronic and temporary foci can be found in this habitat. The aphids can be either pests or economically indifferent species, sometimes the latter fall within the host range of the important *L. testaceipes* parasite. Conclusions: This kind of habitat may serve for pest aphids as well as parasite dispersal routes over the area. Chronic foci may be present. Relations to other habitats: Due to their following the roads, the way-side trees practically are distributed all over the country. This is rather important, they may have relations to the neighbouring habitats as both sources of pest aphids or indifferent species and associated natural enemy food chains are included.

- *Orchards*. Example: Santiago de Las Vegas, Agric. Expt. Station.

Aphids: *Toxoptera aurantii* - *Calophyllum antillanum*, *Citrus* spp., *Annona reticulata*, *Theobroma cacao*, *Ruellia paniculata* (undergrowth). *Aphis craccivora* - *Crotalaria lanceolata* (undergrowth). Parasites: *Lysiphlebus testaceipes*.

Example: Jovellanos, prov. Matanzas.

Aphids: *Pentalonia nigronervosa* - *Musa* sp.; *Toxoptera aurantii* - *Citrus* spp. Parasites: *Lysiphlebus testaceipes*.

Example: Alquizar, Habana prov.

Aphids: *Aphis coreopsidis* - *Bidens pilosa* (undergrowth), *Aphis spiraeicola* - *Citrus* sp.; *Toxoptera aurantii* - *Citrus* sp. Parasites: *Lysiphlebus testaceipes*.

Analysis of examples: Monoculture orchards represent habitats where temporary foci of parasites, both on the crops or in the undergrowth, may be found. On the contrary, mixed orchards may include chronic parasite foci (undergrowth, ornamentals, etc.). *Toxoptera aurantii* and *Aphis spiraeicola* are the main orchard pests. Of the parasites, *Lysiphlebus testaceipes* is the most important, attacking a number of both pest and indifferent aphid species.

Conclusions: Orchards have some features of forest-type habitats, however, their plant composition is different. They include temporary or chronic foci of parasites and sources of aphids in dependence on the type of the orchard. Mixed orchards seem to be more useful as to the parasite occurrence. Relations to other habitats: Although having many different features, the orchards exhibit many characteristics of forest type habitats. On the other hand, many species associated with herbs may be found in the undergrowth. These two basic features determine the orchard qualities with respect to pest species and their parasites: forest type pest species distinctly prefer orchards for a certain part of the season, they may or may not also occur on various plants in the undergrowth; for this reason, pests may occur in the habitat almost throughout the year. On the other hand, undergrowth may include various plants which are associated with indifferent aphid species - alternative hosts of useful parasites. Their occurrence in the undergrowth gives them a possibility to attack the pest aphids both when they invade the orchard or occur in the undergrowth as well. The same is true of the neighbouring habitats (way-side trees, ornamentals).

- Pastures. Example: Rancho Luna, Las Villas prov.

Aphids: *Aphis craccivora* - *Ghiscidia sepium*; *Aphis nerii* - *Callotropis procera*. Parasite: *Lysiphlebus testaceipes*. Analysis: Aphids are comparatively rare, being mostly attached to hedges, etc. Chronic or temporary foci of parasites can be present. *L. testaceipes* is important. Conclusions: This habitat is relatively poorly inhabited both by aphids and parasites; aphids are mostly associated with ruderal elements or with hedges. Hedges might be important in spreading some aphids and parasites.

Example: Chivirico, Oriente prov.

Aphids: *Aphis coreopsidis* - *Bidens pilosa*; *Aphis nerii* - *Callotropis procera*; *Aphis spiraeicola* - *Eupatorium* sp.; *Dactynotus erigeronensis* - *Erigeron canadense*; *Hyperomyzus lactucae* - *Sonchus oleraceus*; *Myzus persicae* - *Emilia sonchifolia*. Analysis: Aphids are rare except for weed and ruderal plants on which they are common, both pests and indifferent species being present. Parasites: *Lysiphlebus testaceipes*. Temporary foci of parasites are present. Conclusions: Occurrence of aphids and parasites is low in this habitat. aphids are mostly associated with ruderal and weed plants. Relations to other habitats: Practically pastures are related most to savanna (cultivated), many weed and ruderal plants being present as well.

- Sugar cane and maize. Example: Guanabo, Habana prov.

Aphids: No aphids on *Saccharum officinarum*, *Sipha flava* were found on neighbouring *Andropogon caricosum* growth. Parasites: No parasites reared. Analysis: The aphids may seasonally occur in other grasses being a seasonal pest on cane. No chronic foci of parasites were established in the field. Conclusions: *Sipha flava* is a seasonal pest on cane, occurring in various sources in the neighbourhood of plantations. No parasite foci of a chronic type occur in the cane fields.

Example: Catalina de Guines, Habana prov.

Aphids: No aphids on *Saccharum officinarum*. *Zea mays* - *Rhopalosiphum maidis*. Environs: *Aphis craccivora* - *Vigna sinensis*, *Gliricidia sepium*; *Pentalonia nigronervosa* - *Musa paradisiaca*; *Aphis spiraeicola* - *Citrus* sp.; *Aphis gossypii* - *Capsicum* sp.; *Hysteronura setariae* - Gramineae; *Toxoptera aurantii* - *Citrus* sp. Parasites: *Lysiphlebus testaceipes*. Analysis: occurrence of aphids on cane is seasonal. They spread to cane from the neighbourhood—wild grasses, Indian corn fields, etc. Chronic foci of parasites occur in the cane field neighbourhood. Conclusions: Due to the absence of parasites in cane fields, the parasites must spread to the fields from the neighbourhood; as the aphids attacking cane are present on various other plants in the neighbourhood, they can be and are attacked here by parasites (chronic and temporary foci). Relations to other habitats: Field landscape itself is very specific. On the one hand, there are extensive areas of monocultures, on the other hand there are numerous remains of various habitats, virgin lands to waste places. All this often causes rather complicated relations, which must be dealt with separately: Relations within the crop field, relations between the different crop communities, relations between the crops and forests, way-side trees, savanna, waste places, etc., due to the often unstable character of field habitats (annual crops, etc.) the mutual dependence of the separate communities is very strong.

- Ruderals. Example: Generalized from various samples.

Aphids: *Acyrtosiphon bidenticola* - *Bidens pilosa*, *Aphis coreopsidis* - *Bidens pilosa*; *Aphis craccivora* - *Boerhavia diffusa*, *Crotalaria lanceolata*, *Tribulus* sp., *Pisonia aculeata*, *Portulaca oleracea*, *Lepidium virginicum*; *Aphis gossypii* - *Boerhavia diffusa*, *Commelina* sp., *Ruellia paniculata*, *Tridax procumbens*, *Waltheria americana*, *Sida acuminata*, *Eleusine* sp., *Cucumis dipsacus*, *Malvastrum coromandelianum*; *Aphis nerii* - *Callotropis procera*; *Aphis spiraeicola* - *Bidens pilosa* (rarely), *Echites umbellata*, *Eupatorium* sp.; *Dactynotus ambrosiae* - *Sonchus oleraceus*, *Parthenium hysterophorus*; *Dactynotus erigeronensis* - *Erigeron canadensis*; *Dactynotus* sp. - *Tridax procumbens*; *Hysteronura setariae* - *Andropogon gracilis*, *Setaria viridis*, *Chloris inflata*; *Hyperomyzus lactucae* - *Sonchus oleraceus*, *Myzus persicae* - *Emilia sonchifolia*, *Solanum* sp.; *Neomyzus circumflexus* - *Eupatorium* sp., *Tetraneura hirsuta* - Gramineae, *Panicum* sp.; *Toxoptera aurantii* - *Eupatorium* sp., *Ruellia paniculata*. Parasites: *Acanthocaudus tissoti* - *Dactynotus ambrosiae*; *Aphidius floridaensis* - *Dactynotus ambrosiae*, *Dactynotus erigeronensis*, *Dactynotus* sp.; *Diaeretiella rapae* - *Myzus persicae*; *Lysiphlebus testaceipes* - *Aphis coreopsidis*, *A. craccivora*, *A. gossypii*, *A. nerii*, *A. spiraeicola*, *Hysteronura setariae*, *Toxoptera aurantii*. Analysis: Temporary foci of parasites are present, however, due to the number of plant species and aphids they often have a rather long-termed character. Pest aphids: *Aphis craccivora*, *A. gossypii*, *A. spiraeicola*, *Myzus persicae*, *Hysteronura setariae*, *Toxoptera aurantii*. Aphids - alternative hosts of useful parasites: *Aphis coreopsidis*, *A. nerii*. Indifferent aphids - *Dactynotus* spp., *Tetraneura hirsuta*, *Acyrtosiphon bidenticola*, *Hyperomyzus lactucae*, *Neomyzus circumflexus*. Conclusions: Aphids are often present on various weeds on ruderals. Of these, many are pests. Ruderals, therefore, often represent long-termed sources of pest aphids. Foci of parasites are temporary but long-termed; due to their common occurrence in such places the parasites may attack a number of aphids here and may reduce the number of pest aphids present too. Relations to other habitats: Practically, as they follow man, ruderal elements are present everywhere. Nevertheless, they are more common in waste land and roadsides than in virgin land. Their presence everywhere makes them extremely important because, moreover, they are mostly attacked by various polyphagous aphids, who are common pests of crops as well. Only a minor part of the ruderal flora includes plants with which specialized

aphids are associated. These features illustrate the numerous relations of the ruderals to neighbouring habitats: Pest aphids often occur here and ruderals are their common and rich sources; ruderals are practically uncontrollable by chemicals; on the other hand, parasites—due to the number of occurring aphids—are common on ruderals and may attack a large number of pest species present; from the latter point of view, ruderals might be sometimes classified as “traps” for pest aphids.

—Classification. 1. Wild and cultivated habitats. The original floristic associations and communities have been widely suppressed or at least deeply touched in Cuba due to the influence of man. The natural communities may be found commonly in areas not suitable for agriculture (dry forest, mangroves, etc.) and in some parts of the mountain districts, where the deforestation has not been so intensive. Nevertheless, the original communities have not been eradicated in the cultivated areas. Although the fields and plantations of various crops are numerous and cover a great acreage of land, the native flora may be found in some remains (no tillage) of native communities at the borders of roads, fields, etc., being of course more or less influenced by the new (ruderal and cultivated) elements. On the contrary, due to the climate and spread possibilities, the cultivated crops either invaded or were introduced in the forests and some of them have become wild (Citrus) as the forest community was very useful and similar to their original habitat.

Therefore, wild and cultivated habitats cannot be strictly separated from each other in Cuba similarly as in every intensively cultivated (island) area. The penetration of separate elements is various. This feature of habitats is important both for the spread of pest aphids and biological control.

2. Forests. All types of forest are important for the pest aphid biological control in Cuba. The mountain forest, but sometimes also the lowland forest, includes a number of aphids—also pest species—and represents on the one hand the continuous source of pest aphid species in the Island; on the other hand, due to the number of both pest and indifferent aphids occurring in the forest, the parasites (native and introduced) can or will find suitable conditions and hosts here. The forests then represent important sources and include foci of parasites from where they can spread and survive here also in case of unsuitable conditions existing in the savanna (dry period). The newly introduced parasites have also to be liberated in various forest type habitats to be established also there.

3. The savanna districts of Cuba are today mostly cultivated, maize and sugar cane mostly being grown. A number of aphids may be classified as being typical for this type of habitat (*Rhopalosiphum maidis*). Although the foci of parasites are mostly temporary here, either some chronic foci in naturally irrigated places (brooks, etc.) occur or the parasites follow the aphids to similar types of habitats (another field, Indian corn). Because of these features the parasites are not so more or less uniformly spread in the steppe as in the forest, but the wet places mentioned are more rare and the parasite must gradually spread from such places into the cultivated fields.

4. Way-side trees are very important for the spread of aphid parasites in Cuba. Being grown along the roads over the Island, they represent good routes of parasite spread, which is believed to follow the host in the majority of cases. Of the way-side trees, *Glicidia sepium* and *Nerium oleander* seem to be the most important. *Glicidia sepium* is the most common and widely distributed way-side tree in Cuba. It is mainly used in the following ways. The cut-off branches are used for new fences or hedges, they soon grow and a new pasture *Glicidia* avenue is the result. Then the cycle is repeated. As this practice has been commonly used by farmers almost all over the Island since ancient times, *Glicidia* may be found lining the roads, pastures, gardens, etc. from the lowlands to rain forests in Cuba. The commu-

uous cutting of branches results in producing new young branches on the trees, so that in a certain period of the year the trees all over the country are cut and young branches appear. Naturally, the viciaceous trees, for instance, with a lot of young sprouts and branches, represent splendid food sources for *Aphis craccivora*. During the dry winter especially the trees are really covered with these aphids everywhere. In addition, *Gliricidia* is a very useful honey-plant. These features can be summarized as follows for the purpose of biological control: (1) *Gliricidia* trees are commonly grown anywhere from the lowlands to the mountains in Cuba, being economically valuable because of wood-production and being honey-plants. The trees are widely used as way-side trees so that their occurrence is trans-zonal, (2) For a long time, and in some months the more, they represent sources of *Aphis craccivora*, (3) This aphid was found to be an occasional pest on some crops in Cuba, but it is believed to be mostly a more or less indifferent aphid species (except for the Viciaceous crops), (4) *A. craccivora* is a member of the *Aphis* group to which the main aphid pests in Cuba belong, so that it is most probable that the parasites attacking this aphid will attack the other related species and vice versa. These conclusions can be used in biological control praxis: (1) In conservation and spread of native parasites, this process is more or less incidental, (2) For the spread of introduced parasites, (3) The introduced parasites must be colonized at a suitable period—when there are *A. craccivora* present in great numbers on the trees. In a neighbouring island, Isla de Pinos, only trunks of palms are used as hedges or fences in pastures instead of *Gliricidia*. According to our opinion based on the classification of *A. craccivora* as an occasional pest but a useful alternative host of a number of parasite species (introduction program), this feature seems to be negative. *Gliricidia* is recommended to be used in this island in a similar way as in the Island of Cuba. *Nerium oleander* is commonly grown as an ornamental in towns, villages and recreation places on the sea-shore. Nevertheless, in several places it was seen to be grown as a way-side ornamental, too. It is commonly attacked by the entirely indifferent *Aphis nerii* all over the Island. The shrubs of the oleander should be used for biological control purposes in a similar way to the *Gliricidia* tree. When comparing the next way-side tree, i.e. *Bursera simarouba*, which is also commonly grown in some parts of the Island, it is obvious that this is not a suitable tree as it is commonly attacked by the pest aphid *Aphis spiraecola* and sometimes also by *Toxoptera aurantii*. However, because of the common occurrence of this tree in the forests, and also due to its economic significance, the tree cannot be eliminated or eradicated, moreover the aphids are widely polyphagous and may occur on a number of other host plants. *Calophyllum annilinum*, a source of *Toxoptera aurantii* namely, is a similar case.

5. Weeds. Some weeds might be important in the temporary foci of parasites for the conservation of parasites, both native and introduced species.

6. Ornamental plants are very important for biological control praxis. They are (1) commonly grown all over the Island, mostly in irrigated places, (2) mostly commonly attacked by polyphagous aphid species, (3) in some cases they have peculiar aphid fauna (*Nerium*). Because of these features their importance is obvious. They represent food plants of aphids in the chronic foci, in continuously and carefully irrigated land. These districts are very important, just because of the continuous occurrence of the host aphids, for the colonization and establishment of introduced parasites.

7. Irrigation places. All the irrigation places, both accidentally or artificially irrigated, are very important for biological control. Because of the irrigation, plants of all kinds, crops and weeds, successfully grow here, are useful hosts for various aphids (and associated food chains). Introduced parasites should be released

mainly and primarily in such places where there is a good possibility of establishment.

ZONES. Climatic influences and zonation are the main factors that determine the distribution of plant cover of the earth and, simultaneously, the distribution of aphids and their parasites. Although each floristic zone exhibits certain peculiarities with respect to the parasite fauna, it is possible to summarize the peculiarities of parasite foci in the general climatic zones.

– *Temperate zone.* In connection with peculiarities in aphid and parasite biologies this zone seems to be the most typical as to the apparent and well-developed habitat dependence in parasites. The fauna of parasites is the richest here, this being the result of evolution of the group as a whole. The characteristics of the foci are determined by the mentioned features; species occurring in various foci are numerous, and the foci generally may be well distinguished. Natural communities exhibit a relatively rather stable character, while cultivated land may be both stable and unstable environments. Seasonal influences are apparent, a cold or milder winter has a rather deep influence on the seasonal occurrence of aphids and parasites as well as on the development of quiescent states. Aphid life-history, besides hibernation, exhibits also peculiarities such as obligatory host alternation, a factor that is rather important as to parasite foci.

– *Subtropics.* The Subtropics seem to have an intermediate character. On the one hand, there may be found, at least partially, many features known to occur in aphid and parasite biologies in the temperate zone, such as obligatory host alternation by aphids and strict habitat dependence by parasites; on the other hand, peculiarities that are typical for the subtropics and tropics can be found too. Some aphid species may exhibit less habitat dependence during the season, some aphids may reproduce parthenogenetically during the whole year. All these features have a corresponding significance as to the foci of parasites. While the winter is usually rather mild, the critical period is the hot dry summer with many adverse influences on the aphid and parasite fauna, adaptive responses having developed in consequence. Seasonal influences are rather apparent, many aphids and parasites occurring in the course of the whole year, in evergreen communities and irrigated land for example.

– *Tropics.* Because of the climatic features of the tropics, the parasites do not seem to depend in such a close way on the type of habitat as they do in the mild climate zone. This seems to be also a result of the specific composition of the fauna as well as the evolution of the group. The occurrence of aphids and parasites is perennial. Dry and rainy seasons of the year seem to exhibit different influences in evergreen and non-evergreen floristic associations. This feature is important also for the character of parasite foci: chronic foci seem to be prevalent in the evergreen associations, while temporary foci are typical for non-evergreen associations as well as cultivated land. However, the dry season may cause a relative concentration of aphids and parasites in certain plots, where the temporary foci may be relatively long-termed as to their existence.

being apparently accidentally introduced into greenhouses, and unable to disperse and survive perennially under field conditions. This parasite was classified as probably a peculiar race of the parasite (SCHLINGER & MACKAUER, 1963) as another race of the same parasite species has been able to spread over certain districts of California, being apparently introduced as well.

In milder climate areas the unheated greenhouse conditions may exhibit similar features as heated greenhouses in colder areas. Both aphids and parasites were observed to reproduce here throughout a mild winter, although they were hibernating in the field (DUNN, 1949).

As was shown in another chapter, the greenhouse aphid fauna represents mostly species that are unable to overwinter in the given temperate district outside the greenhouse, while living for certain warmer parts of the season in the field as well—mostly in the greenhouse neighbourhood. As in most cases the parasites attacking such aphids are not introduced into the given country, being members of the communities of the greenhouse neighbourhood, unnatural food chains in greenhouse conditions originate. Similarly, due to the continuous aphid and parasite occurrence in greenhouse environment, the foci of parasites must be classified as being of the chronic type, although artificial as to their original character.

The incidental role of greenhouses as parasite foci has lead us to the idea as to whether they could not be used purposely as the foci in the biological control program. In this respect, for the time being, we have proposed (see biological control chapter) on the base of our preliminary experiments, to use small unheated greenhouses in a parasite introduction program in the cooler districts to enable the parasites to occur earlier in the season. Indigenous parasites, too, can be manipulated in a similar way.

ARID ZONE. Arid zone includes extensive territories, associated previously with steppe, semidesert and desert areas, including naturally various other elements. Arid zone conditions are rather peculiar and have deeply influenced the indigenous fauna both as to its specific composition and seasonal history. A basic character of an arid zone is the relative scarcity of water, seasonal rains and extremely hot and dry and sometimes cold conditions occurring in certain periods of the season. This state has naturally caused deep adaptation in the flora and fauna. On the one hand, there is a rather significant and well-defined seasonal succession of plant communities associated with seasonal changes in insect fauna, on the other hand, reservoirs of water exhibit peculiar features. Aphid fauna also is rather unusual (IVANOVSKAYA, 1959, 1960, 1961, LOZOVY 1961, SHAPOSHNIKOV 1952, MARIKOVSKIY, 1955, etc.), its many members being typical xerobionts. The same is true as to parasites. Foci of parasites have the same features. Many of them are temporary, chronic foci being associated mostly with sources of water (STARÝ 1965).

Cultivated land is rather common today in an arid zone. Its appearance has caused deep changes in its own fauna and in the environmental fauna as well, as the cultivation in arid land is mostly connected with extensive irrigation and microclimatic changes. This feature has been studied by a number of authors (SMITH 1959, UVAROV 1962, BEY-BIENKO 1961, and others). Generally, according to the summarizing paper of UVAROV (1964), the fauna of cultivated crops in arid land is composed both of the typical widely distributed species associated with the given crop, and of the elements of the original arid land communities that have adapted to the new environment, while a certain part of the original indigenous fauna did not survive the changes and was eliminated. Aphids are undoubtedly a group of insects which has found irrigated monocultures to be a rather suitable source of food and many aphid species dispersed

from the arid land neighbourhood to cultivated land and became pests; besides, a number of widely distributed pest species accompanied them, when following cultivation and growing the given crop in new land. Similar features may be observed in the composition of parasites. The fauna of parasites is composed both of indigenous steppe-desert species and of widely distributed parasites. Foci of parasites on cultivated land are various. Many of them are temporary, occurring in annual crops, but there are a number of chronic foci just in irrigated land, especially near the water sources, in connection with complex communities occurring in such places. Other chronic foci can be found in perennial crops too (alfalfa).

— RELATIONSHIP. Cultivation in an arid zone is connected with the irrigation of virgin arid land, i.e. with virgin steppe and namely semi-desert and desert areas. Irrigation means the creation of new habitats, where on the one hand humidity conditions occur which are favourable to a number of insects during a hot summer when the semi-desert environment becomes dry, on the other hand, a number of plant crops appear which are grown in monocultures, remaining green in the hot summer.

Aphids and parasites are one of the examples on which the relations on irrigated land and virgin neighbourhood may be well demonstrated. Extensive studies were undertaken, namely in the C. Asian districts of the U.S.S.R. GULYEV (1965), whose observations were carried out in the very same district where also the foci of parasites in the cotton fields were studied by the author (see review of foci) found that the primary sources of pest aphids in the wild neighbouring communities are the greatest dangerous significance for the infestation of cotton fields by pest aphids. For example, the first colonies of *Acyrtosiphon gossypii* and *Aphis gossypii* were observed on the wild semi-desert plants *Alhagi camelorum* and other salsolaceous plants, cotton being attacked after the first young leaves appeared. Parasites of the aphids dispersed in a similar way.

Extensive observations undertaken just in the direction of the research of pest aphids with respect to semi-desert and irrigated landscape were presented by DAVLET-SHINA (1956). This author showed on examples of cotton aphids in Soviet C. Asia the seasonal occurrence of pest aphids on crops, namely cotton and the decisive role of wild environments as aphid sources. The research is so detailed and so many examples and observations are mentioned that today there can be no doubt that the research of foci of both pest aphids and parasites is necessary and a basic condition for successful aphid control.

YAKHONTOV et al. (1962) studied the fauna of "Golodnaya" steppe in Soviet C. Asia, the main interest being paid to different habitats of the desert landscape and relations between virgin and cultivated land. Their results seem to be very valuable and are believed to be applicable, at least generally, for similar arid zone districts. Unfortunately, no parasites of aphids were dealt with, but we ourselves made some research work in allied districts so that our observations can be used here at least as a general scheme. It is obvious from the table that there are in many cases close relations between the natural, old-irrigated and new-irrigated land. This fact clearly shows that the same (pest) aphids occur both in wild and cultivated habitats. In their native land there are their sources, from which they can and do disperse to the cultivated areas on various crops. As potential pests of this type the following species may be mentioned: *Sipha maydis*, *Therioaphis ononidis*, *Sitobium avenae*, *Acyrtosiphon gossypii*, *Myzus persicae*, *Schizaphis graminum*, *Aphis gossypii*, *A. craccivora*, *A. fabae*, *Brassicorhynchus brassicae*, *Brachycaudus helichrysi*, *Xerophilaphis plotnikovi*, etc. Very important results were obtained by the authors when dealing with the succession of aphid occurrence on newly grown crops in one and two-year old fields in newly cultivated

virgin steppe. The main crops grown in newly cultivated areas are cotton, alfalfa and maize, while the environmental virgin steppe is of *Artemisia-Salsolacous-ephemerie* plant type. The cultivation of virgin land and the growing of new crops exhibits a strong influence on the specific composition and number of insects. Some species disappear or their population density is much lower, while the density of other species becomes much higher. As to the aphids, their number on cultivated land becomes rather high, while some species, such as *Aphis verbasci*, disappear. On cotton fields, *Acyrtosiphon gossypii* and *Aphis craccivora* were found to occur during the first year, their number increasing during the second year. On alfalfa, *Acyrtosiphon pisum*, *Aphis craccivora* and *Therioaphis ononidis* were found in great numbers during the first two years of crop-growing. In old cultivated land in C. Asian oases, the fauna of aphid pests is well established and known. During the research of weed and wild plants in the neighbourhood of fields, *Aphis craccivora*, *A. gossypii* and *Dactynotus sonchi* (indifferent species) were found.

- IRRIGATION. In connection with irrigation of certain districts of arid land, foci of parasites have originated as well in such districts though they had been rare or absent previously, as we can judge according to the research of virgin land. However, cultivation of arid land resulted also in growing crops in monocultures on extensive areas, where the foci were absent due to the elimination of weeds and uncultivated land, the occurrence of chronic parasite foci inside the crop being relatively rare (alfalfa). Observations of various authors (LUZHETSKI, 1960) have shown that there is a gradual and slow dispersal of parasites to cotton fields attacked by host aphids. This is fully recognizable from our concept of classification of foci: in cotton fields, there are no chronic foci; the parasites disperse only gradually to cotton from the foci in the neighbourhood. Similarly, as we have observed during our research in C. Asia, there are various relations between different crops, as to the parasite foci: *Acyrtosiphon pisum* on alfalfa, and *A. gossypii* on cotton have some identical parasites, the chronic foci being present in alfalfa fields, a perennial community. Therefore, generally we have the same problems on irrigated land in an arid zone as in other zones; however, it seems that pest species occurrence in irrigated land is supported by the rather unsuitable conditions that occur in the virgin neighbourhood during certain periods of the year.

- FOREST PROTECTIVE BELTS. Forest protecting belts are grown in arid land with the aim of changing climatic conditions in favour of cultivated crops. The appearance of forest elements in steppe and semidesert land has naturally caused new relations respecting the fauna both of aphids and parasites. Besides the appearance of typically forest species of aphids, many species of steppe aphids also found the belts to be suitable. In consequence, certain trees and other plants grown purposely or accidentally in forest belts are known today to be sources of some pest aphids, while other species were eliminated due to climatic changes. *Aphis craccivora* is an example (MAMONTOVA, 1957, USFENSKI, 1951): *Caragana arborens* and to a lesser degree *Robinia pseudoacacia*, two woody plants grown in the belts, were found to be main host plants of this aphid, from which it disperses to the neighbouring cotton fields, heavily attacked by the pest just in the neighbourhood of the woody plants mentioned. *Ulmus* trees are a similar case (MAMONTOVA, 1956) having relations to corn through *Schizoneura* pest-aphids. Unfortunately we have no records on the parasites from the areas where the above observations were made. However, in smaller arid districts of C. Europe (Czechoslovakia-southern districts), where forest protective belts are also grown, the habitat dependence of parasites is the same as in the neighbouring forests, i.e. the forest belt parasite fauna is mostly strictly separated from that in the fields. According to our observations in C. Asia, however, certain parasite

species typical of steppe habitats (in C. Europe) may also attack aphids living on shrubs and trees similarly as species associated with forests (in C. Europe) may be found dispersed in semi-desert or irrigated land. There is no doubt that the seasonal extremes of the arid zone districts as well as local conditions are responsible for such changes in habitat preference of certain parasite species. Nevertheless, forest protective belts have also a number of positive features, including the presence of chronic foci of many aphid parasites both on woody plants and herbs (honey-plants) grown along the belt. A high concentration of natural enemies is reported to be typical of forest protective belts in general (MELNICHENKO, 1949).

— INFLUENCE OF HOT WINDS. According to ROSEN (1967), the hot dry hamam desert winds, prevalent in spring in Israel, contribute considerably to the early decimation of spring populations of *Toxoptera aurantii* on Citrus and most of the colonies are usually destroyed even before the parasites start their attack. Due to such influences of desert winds on the aphid fauna, we can anticipate that such winds will similarly influence the parasite foci, although it is known that both Citrus crop and associated aphid pests are not native to the part of the arid zone mentioned, so that better adaptation could exist in the indigenous fauna. Unfortunately, no records are known in this respect and research is necessary.

CONSERVATION. Our knowledge of parasite foci in nature has shown that they are not of equal importance for man, many of them being entirely indifferent. Thus any proposal for the protection of parasite foci must be based on detailed analysis of the host plants, host aphids, complexes of parasites of the given foci, i.e. after the structure and character of a given focus becomes evident. We must distinguish the foci existing inside the given crop culture, in allied crops, and in neighbouring areas such as uncultivated land, hedgerows, etc.

Recommendations for protection of foci should not come into conflict with more important activities, e.g. weed control, etc. Several illustrative examples can be presented:

Example: *Sarothamnus scoparius* growth in C. Europe. In some areas, on waste places, roadsides, edges of woods, etc., the growth of *S. scoparius* is rather common. Besides specialized *Aphis* species, *Acyrtosiphon spartii* is commonly associated with it; this aphid is an alternative host of *Aphidius ervi*, which is a partially effective parasite of *Acyrtosiphon pisum* pest aphid on alfalfa. As *Acyrtosiphon spartii* is a monoecious aphid, being also heavily parasitized by the parasite in certain parts of the season, the *Sarothamnus* growth may be classified as useful for parasite occurrence, representing its chronic foci.

Example: *Cirsium arvense* — weeds in C. Europe. We shall not protect its growth, as it is a weed and moreover a secondary host plant of the pest *Aphis fabae*. Although the aphid is often heavily attacked by the parasites on this plant, basic research has shown that its parasites can attack other economically indifferent aphid species in the same habitats, which include both temporary and chronic foci.

Example: *Artemisia* and *Achillea* plants are common weeds in C. Europe, they can be found in waste places, roadsides, hedges, etc. However, basic research of this type of foci has shown that the aphid fauna and associated complexes of parasites are rather specialized, having no relation to pest aphids. Thus the growth of these plants need not be protected from the viewpoint of parasite fauna conservation.

It must be added that also other groups of entomophagous insects must be taken into consideration, as, for example, the aphid species which are indifferent to parasites can be rather important as alternative prey of predators.

Example: Citrus orchards in Italy. Citrus is grown either in monoculture or

in Citrus orchards and their neighbourhood, it is projected to replace *Pittosporum* shrubs with other ornamentals: (1) Oleander (*Nerium oleander*); its main pest, *Aphis nerii*, is one of the preferred hosts of *L. ambigua*. Oleander is a common ornamental plant the same as *Pittosporum* is, but *Aphis nerii* does not attack Citrus; (2) The willow (*Salix* spp.) seems to be also a very suitable tree. It is attacked by specialized *Aphis farnosa*, which is one of the main hosts of *L. ambigua*. The growths, belts, etc., of both plants mentioned represent chronological foci of the rather effective *L. ambigua* that disperses from them to Citrus orchards and can attack *Toxoptera auranitii* as well. Besides, it attacks also *Aphis punicae*, as pest on *Punica granatum*, and other pests (*Aphis craccivora* for example); (3) In Citrus orchards, the occurrence of grassy and weedy undergrowth may be supported as the *Aphis* spp. occurring there mostly represent also hosts of *L. ambigua*. Nevertheless, in case of complex treatment, the undergrowth fauna is affected by the chemicals as well.

Example: Peach orchards (S. Italy). *Hyalopterus pruni* is one of the main aphid pests, causing curling and drying of leaves. *Prunus* spp. are its primary hosts, while *Phragmites communis* is the main secondary host plant. The aphid can be found both on the primary and secondary host plants in orchards and gardens, i.e. in habitats of the same kind. It is attacked by two parasites species—*Aphidius transcaspicus* and *Praon volucre*. *A. transcaspicus* is distributed in southern Europe, the Mediterranean, and C. Asia, occurring in orchards and gardens or on reeds, attacking *Hyalopterus pruni* and *Longunignis donacis*. *Praon volucre* is distributed from Europe to C. Asia, being a comparatively widely eurytopic species, occurring in orchards, and gardens, sometimes in fields and steppes, too, its host specificity being of a wide range.

Hyalopterus pruni migrates to peach trees from the secondary host plants of which *Phragmites communis* is the most important, or from other host plants—weed trees like *Prunus spinosa* or other *Prunus* spp. (*P. domestica*, *P. armeniaca*). *Phragmites* thickets are common in the neighbourhood of orchards in irrigation ditches and various smaller or more extensive marshes or ponds formed by irrigation. *Prunus spinosa* is planted sometimes as hedges. For the reason mentioned above it is recommended to cut down the *Phragmites* thickets and *Prunus spinosa* should be considered unnecessary where possible. *Hyalopterus pruni* is attacked on the host plants mentioned by the same parasite complex as on the peach trees, but in connection with the pest existence and its dispersal to peach trees foci of this type in a nearby neighbourhood of orchards must be considered as unsuitable. In the same type of habitat (reeds on marshes, ditches, etc.) as *Phragmites*, *Arundo donax* reed is commonly found. According to our observations this reed is attacked very slightly by *Hyalopterus pruni* while *Longunignis donacis* is rather common and *Schizaphis longicauda* less common on this plant. *Longunignis donacis* is a preferred host of *Aphidius transcaspicus* that can be found here too, and from here it spreads to the neighbourhood where it attacks *Hyalopterus pruni* on *Phragmites* or in orchards on peach trees. Therefore, *Arundo donax* thickets represent a chronic type of foci, the occurrence of which should be supported, as its aphidofauna includes economically indifferent species and represents alternative host of *Aphidius transcaspicus*, a partially effective parasite of *Hyalopterus pruni*.

RESEARCH TRENDS. The research of parasite foci undoubtedly represents a very important trend of research of parasite biology.

Basic research covers the classification of foci, relations between aphids and parasites in field conditions both as to their occurrence and seasonal history, dispersal of aphids and parasites with respect to the relation among natural and cultivated areas, effectiveness of parasites in various habitats, etc. As it is obvious, such a type

of work requires a high level of taxonomic research which is the prerequisite to avoid mistakes in the research of foci.

Applied research of foci is connected with the research of parasites of a certain pest aphid so that it is usually much narrower as to its scope. It needs at least a basic knowledge of the theory of the foci and rough orientation of the worker in the field conditions of the area in which the research is to be undertaken. The knowledge of aphid biology, its occurrence in various habitats during the season and its seasonal occurrence in general are rather helpful to eliminate a number of various habitats which would be naturally dealt with during more complex research. Basic information concerning the parasite host specificity influencing factors allows a more detailed search for various alternative hosts. A special topic of the applied research is the occurrence of introduced parasites and their relation to the foci in the new country, alternative host problems, etc. In this case, too, at least general information on host specificity of parasites may be rather useful.

SCHEME OF RESEARCH. In connection with the trends in research of foci two different schemes can be mentioned in accordance with whether they have to be used in basic or applied research.

- *Basic research.* 1. The main types of landscape of the area studied are selected.
- 2. Main types of biogeocenoses or ecosystems in these landscapes are distinguished, principally regarding the character of habitat and plant community.
- 3. Samples of aphid species present in these main biogeocenoses are taken in various parts of the season, the parasites being reared. All obtainable aphid colonies are collected to get as many records as possible.
- 4. On the basis of results obtained in this way, the analysis of separate biogeocenoses is undertaken, main types of habitats selected and faunistic complexes of parasites established.
- 5. Main types of habitats with respect to the classification of foci are selected and mutual relations established.

As a result of the basic research, all the main habitats present in the given area have to be known in order to obtain information of the indigenous parasites with respect to a given aphid species.

- *Applied research* starts with a given aphid pest species and requires information on indigenous parasites, their effectiveness and possible role in control. Samplings for such research are concentrated mainly to the given aphid species, while allied information on separate parasite species, their alternative hosts, etc., is a further step towards research.

- 1. Life-cycle of the given aphid species and its occurrence in various types of habitats.
- 2. Sampling of all obtainable colonies of the aphid in separate kinds of habitats in which it occurs.
- 3. Analysis of parasite composition.
- 4. Selection of the most common and effective species and their classification in accordance with the data obtained in basic research.
- 5. Establishing of foci of these parasites in nature and field information on their effectiveness, dispersal, etc.
- 6. Classification of habitats with respect to the introduction of other parasite species from abroad.

Further activities are connected with biological control and integrated control programs.

BIOLOGICAL CONTROL.

– *Release of introduced parasites.* The basic idea of the biological control program in introducing parasites is to make them new permanent members of certain communities in a given country to control a given pest species. For this reason, release of introduced parasites must be made simultaneously or gradually both in the given cultivated crops in which the pest is to be controlled and in the neighbouring habitats. The establishment of an introduced parasite in various both wild and cultivated communities gives a greater possibility of surviving various unsuitable periods and of avoiding the elimination of the introduced species in a given country. Therefore, the classification of the neighbourhood besides the planned release plot in a cultivated field has to be evaluated with respect to the known or expected range of introduced parasite specificity and its requirements as to the occurrence in various habitats.

– *Recovery.* If the introduced parasites were released in the cultivated and/or wild neighbourhood or not, search for recovery should be undertaken in all the environments to which the parasites can disperse. This is important, in order to ascertain the gradual adaptation of the parasite in the new environment from which it may disperse to other areas.

– *Establishment.* Generally, a successfully permanently established parasite should occur in the new environment in an adequate way as the indigenous parasites do, i.e. to occur both in wild and cultivated habitats. The strict attachment of a parasite species to a single crop gives it a poorer chance of surviving certain unsuitable periods due to climatic conditions, man's activity, etc. This situation is somewhat better in case that the crop is a perennial and relatively stable community such as alfalfa (Example: *Aphidius smithi*—*Acyrtosiphon pisum* in California). Naturally, this depends on the origin and relations of the pest species controlled, range of parasite host specificity etc., there is no doubt that introduced parasites of *Aphis* spp. and allied groups are expected to find various alternative hosts in the new environments more easily than the relatively strictly specialized parasites, such as those of the Callaphidid aphids, etc.

INTEGRATED CONTROL. This is to give a brief review of the problems, as they are dealt with in connection with other problems in the integrated control chapter in a more detailed way.

– *Inside a given crop.* 1. Complex treatment of a crop by a non-selective insecticide means elimination of parasite foci in the treated plot.

2. Partial treatment. In the treatment of a plot of a field or orchard, parasite foci can be conserved in untreated parts and the parasites may gradually disperse to the treated area and attack either the surviving or re-occurring aphids. Partial treatment may be carried out in a part of a crop growing area, or only the pest outbreak plots can be treated. Similarly, it may not be done in plots where there exists a high level of parasite occurrence. In other cases, the central part of a field can be treated while the field edges are left untreated as these are the areas of parasite dispersal to the field from the neighbouring habitats.

3. Strip treatment is an intentional program to conserve parasite foci in a part of the crop growing area.

4. Selective insecticides, both in dosage or in action, are useful in conservation of either temporary or chronic parasite foci.

5. Timing of treatment. Parasites were generally found to be most capable of surviving treatments when inside mummified aphids, i.e. in last instar larva to pupa stages. Timing of treatment, including the period of insecticide residue action, to a period when the parasites are inside mummified aphids may well preserve the parasite

foci, although a certain part of parasite adults or lower instar parasite larvae (inside the living aphids) may be killed by insecticides. Timing of treatment can be done generally either with respect to their general occurrence during the season or to their developmental stages which prevail in a given period.

6. Weeding in crop growing plots is a generally accepted part of an agrotechnical program. For this reason, weeds in crop growing plots apparently play hardly any role in an integrated control program, although some of them may be useful as temporary foci of parasites. There is another problem, that of conservation of weeds on adjacent non-cultivated areas, where they may or may not be useful as parasite foci.

7. Strip cutting or a strip harvesting program has been developed as a part of an integrated control program of pest aphids on alfalfa. In principle, it is based on preserving the continuity of stable environment occurrence, i.e. on the preservation of chronic foci of parasites throughout the season. Experiments have shown that an entire simultaneous harvesting of a field is detrimental to parasite occurrence. According to our observations it is also important whether the harvested alfalfa is left to dry in the field (dry forage) or immediately transported from the field (green forage).

8. Clean cultivation and its influence on parasite foci must be evaluated with respect to separate kinds of orchards and climatic belts. When being done during the season, clean cultivation may be indifferent to parasite foci in the case that the parasites of fruit tree pest aphids have no relation to aphids occurring on plants in orchard undergrowth, while—vice versa—it may eliminate certain alternative hosts of parasites in the case they attack the aphids occurring in undergrowth as well. Clean cultivation made in spring or in autumn may be detrimental to quiescent (overwintering) stages of parasites as they can often be found on fallen leaves on the ground. There are some exceptions (*Trioxys pallidus*) when the parasites partially overwinter on the bark of trees, so that their reduction through cultivation is lower.

9. Tillage means with perhaps no exception the elimination of parasite foci in a given plot. The superfacing of parasite cocoons (overwintering stages) has the same results. Therefore, we can expect no parasite foci occurrence in spring in such places which were ploughed in the autumn, etc. Seasonal tillage, however, may not mean the elimination of the temporary parasite foci in the grown crops.

10. Irrigation means better conditions for plant growing. Irrigated plots, without any doubt, will be more intensively attacked by aphids, various foci of parasites originating in consequence. From this point of view, irrigated plots may exhibit other features than the non-irrigated plots.

11. Strip farming. It is well known that the fauna associated with different crops exhibits various relationships. This is true for the aphid parasites as well. In the case of strip farming, this relationship might be useful in case of identical parasite occurrence on aphids associated with two different crops, annual and perennial crops, etc., so that one crop field might represent an area where parasite foci are conserved, while they may be reduced in the neighbouring field. However, these relations are specific and may be elaborated only after careful comparison of aphid and parasite specific composition, seasonal history features, etc.

— Between different crops. 12. Intercropping, if undertaken with respect to integrated control, can mean the creation of temporary or chronic foci of parasites in the neighbourhood of a certain crop. Similar conditions seem to occur in this case as well as in the strip farming program. However, it is well known that natural enemies are usually concentrated more on smaller than on larger plots of certain plants.

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orchards. Communities with high species diversity are more stable than simple communities, the crops. Diverse communities may just be found on uncultivated land, which is more or less common in a cultivated landscape. In this uncultivated land many temporary and chronic foci are found, which must be taken into consideration in an integrated control program. However, their specific composition must be dealt with before any similar classification is undertaken as the value of foci is not equal.

14. Hedgerows and forest protective belts have a general character: They exhibit many features of true forest habitats, their parasites may or may not have relation to the adjacent crop areas as to their occurrence and dispersal, however, the aphid pests can be attacked by these parasites if the former are temporarily present in hedgerows and forest belts (dioecious aphids). In addition, hedgerows and forest protective belts do not represent strictly separated habitats, there is an intentionally grown or incidentally developed zone of herbs, such as weeds, honey-plants, etc. This zone of a grassy character usually exhibits great species diversity and may be classified as rather useful from the point of view of parasite foci—both temporary and chronic parasite foci are found here. Besides, many other natural enemies are found here, as well as various adult parasites feeding on aphid honeydew.

— *Foci of indigenous and introduced parasites.* There seems to be a general rule with respect to an integrated control program: Indigenous parasites are inhabitants of a given landscape and they can survive in various habitats also in case they are eliminated in a given plot through the action of man. It means that the indigenous parasites are less vulnerable as to their occurrence in the case that no suitable program is developed; they can soon be re-established after a conservation program is in use. However, on the contrary, great care must be taken in case of introduced parasites, which are not permanently established in the landscape, their foci often being dependent on the presence of certain crops and the given specialized pest's occurrence. It is known that this feature reduces the effectiveness of introduced parasites in certain areas. For this reason, in introduced specialized parasites, it seems perhaps better—in the initial phase of establishment at least—to develop integrated control in the given crop, while the occurrence of the introduced parasites in other (uncultivated) habitats is a matter of a longer period before they become members of the given community in the field neighbourhood, their temporary or chronic foci possibly developing here.

NATURE CONSERVANCY. 1. *Virgin communities.* The research of foci in virgin or at least relatively virgin communities is the basic step in the classification of foci of cultivated land. Forests, generally being less cultivated habitats when compared with steppe habitats, exhibit comparatively original features. For this reason, besides the problems connected with forest communities, many relations found in orchards can be derived from the research of forests. The same is true of the fauna of hedgerows, forest protective belts, etc. Cultivated steppe and semidesert landscape, especially in intensively cultivated areas, hardly allow us to find a really natural virgin land of the original type. To find such conditions, it is necessary to deal with the problem in districts where the cultivation of virgin land still takes place, certain areas of e.g. the U.S.S.R. being rather useful. However, also in European countries, there are various districts where the original state is more or less preserved by the Nature conservancy activities of man.

Although the fauna and general conditions that can be found today in cultivated landscapes are different from those occurring in the virgin steppe, there is no doubt that just the heterogeneity of plant cover and equilibrium known to occur in the

virgin communities give us at least a general idea of the conditions to which our integrated control program should at least partially be directed.

Therefore, it is one of the aims of applied research work to support the activities connected with nature conservancy as it enables us to obtain a corner stone to which other results could be related.

2. Non-cultivated land. Foci of parasites can mainly be found in non-cultivated land in a cultivated landscape. In this land, species diversity is a typical feature, resulting in relative stability. On the other hand, non-cultivated land includes also sources of certain pest aphids. For this reason, protection of non-cultivated land may have both a positive and negative significance. However, in non-cultivated land, a high limitation of pest aphids by parasites usually prevails due to species diversity.

3. Cultivated land. Nature conservancy has as its aim not only the conservation of virgin land, but it has also the leading role or at least some care in elaborating the program as to the development of a healthy landscape as an environment for human existence.

When we have in our mind the extensive application of insecticides against aphids in different countries and zones, the importance of an integrated control program for nature conservancy in cultivated land is well apparent, just from the point of view in reducing the insecticide application to determined necessary levels. From this point of view, we could classify an integrated control program as to be simultaneously a nature conservancy program in a cultivated landscape: one of the leading principles of this program is just the statement that insects are necessary members of agrobio-cenoses.

4. Conservation through integrated control. Any integrated control program has an adequate positive role in nature conservancy as it is the task of such a program which puts a biological agent as its base, to reach such a community state where the pest species are kept under control of biotic agents, treatments and other activities dangerous to nature conservancy being applied only in case the pest has reached certain levels. Complex non-selective treatments, which are especially harmful to nature, must be avoided according to the integrated control program. Foci of certain aphid parasites, in connection with an integrated control program or at least projects, will be preserved through specific activities. Besides their own primary role, the occurrence and dispersal of useful parasite species, the parasite foci—being simultaneously sources of aphids—are significant for a number of other natural enemies as a source of food (honeydew). In addition, however, the fact must be stressed that the conservation of aphid parasite foci is only a small part of the general integrated control program on a given cultivated crop.

- REFERENCES. 6, 17-8, 35-6, 42, 49, 58, 67, 81, 97A, 103-4, 118-9, 121, 134-42, 175, 186-7, 189, 213, 218, 227-9, 239-40, 272, 277-9, 284, 301, 319, 325-8, 330, 347, 351, 411, 415, 450, 458, 469, 480, 487-8, 502, 511, 515, 518-9, 540-3, 569, 580-5, 622, 630, 634, 678, 679, 709, 714-8, 724, 725, 735-6, 745-6, 749, 765, 792, 803, 805, 813, 815, 820, 854-5, 861, 864-8, 870, 874, 891, 894, 918, 922, 924, 928, 931, 942, 946, 955, 957, 971, 976-88, 1001, 1006, 1008, 1015, 1020-2, 1027, 1031, 1039, 1067, 1079, 1082, 1094, 1101, 1108, 1117, 1122, 1123, 1124, 1125, 1127, 1129, 1130, 1132, 1158, 1160, 1177, 1178, 1188, 1190, 1194, 1218, 1220, 1227, 1229, 1240, 1244-6, 1252, 1253, 1265, 1266, 1269, 1280, 1287, 1311, 1321-2.

Natural Limitation of Aphids

The role of parasites in the natural limitation of aphids is of basic significance. All applied research trend must begin from the knowledge of the ecosystem. We must first know the mechanism of the ecosystem, the position of the parasites in a community, and only on this base can we develop certain control activities. This trend, which was developed independently as a result of the studies of many workers, is followed today all over the world, the ecosystem principle being considered one of the basic principles of integrated control.

Methods

— SAMPLING OF POPULATIONS. 1. The correct selection of a plot in which samples are taken is of great importance. The purpose of plot selection is to take samples which would represent an average with respect to the studied area. The type of the community we have to study influences the selection of an experimental plot to a high degree. In natural communities we select a truly typical place, avoiding ecotone problems. In cultivated crops, we avoid ecotone problems too, but the selection of a plot is easier as most of the crops represent monocultures. Plots should be selected, where no treatments are carried out. In special cases, for example, if we have to study ecotone problems, samples are taken from certain parts of the studied areas and the experimental plot is selected in this special part. In other cases, if we have to study the detailed distribution of a population in a given area, plots are selected in a corresponding manner; for example, if we have to recognize the distribution of populations of host and parasite with respect to prevalent winds, etc., the plots are selected in various parts of the investigated fields.

2. The interval of taking samples depends on time and space. As to the time, here we are in a dilemma: the population counts should be made as often as possible, but they can be rather time-consuming as is the further work with the collected material. Most authors have taken samples at weekly or fortnightly intervals. It is recommended, too, to take the samples at a given period of the day to avoid eventual mistakes due to diurnal activities of the insects.

It is well known that populations are not distributed regularly over a certain plot. As we have to make an average picture of a given plot, it is recommended to divide the plot and then to take samples in diagonals, each sample being taken at a certain distance, or, if the crop is sown or grown in rows (potatoes, sugar beet) samples are taken at regular distances in selected plants (each tenth plant, etc.).

Intervals of taking samples, both as to time and space, must be organized in such a way as not to influence the population numbers. For example, GEORGE (1957) ar-

ranged sampling throughout the season so that every plant was visited once in four weeks. Naturally, this is a case of selected plants, but no such care need be paid to sampling in extensive alfalfa fields, etc.

3. Preservation of samples depends on the kind of method used as well as on the quantity of material collected. The smaller samples may be put directly into alcohol; larger samples are usually anaesthetized, and transferred into large or small bags, fixed with adhesive tape, and they are later selected and counted in the laboratory.

4. Sweeping is a rather commonly used method. Principally, it can be applied in two ways: first, we may do a certain number of sweeps in an experimental plot; the results are relative and cannot be related to a certain defined area. Second, we may intensively sweep a certain defined area by as many sweeps as is necessary; such results may be related to a strictly defined area.

The sweeping method is advantageous for obtaining a large quantity of material during a short time. Moreover, adult parasites can be collected as well. However, the sweeping method reveals rather numerous disadvantages, so that it can be used as an additional method only, owing to the following reasons: (1) It cannot be used if the plants are too low, for example, in early growing alfalfa in spring or in cut alfalfa stands; (2) it cannot be used in rainy weather, in windy weather, or when the plants are covered with dew; (3) time of samples can influence the results as there are diurnal movements of insects over a plant; (4) it is difficult to apply in trees and shrubs; (5) it does not cover the whole material present on a plant, some of the specimens fall down when slightly disturbed, further, the quantity of material swept is different in accordance with the size of a plant, in higher plants less material is collected as the standard net does not cover the whole plant; (6) it cannot be used for many aphid species as many of them do not fall from the plants; (7) swept material includes many parts of plants as well as other insects, molluscs, etc., which could destroy the swept aphids and parasites, at least they make difficulties when the material is selected in the laboratory.

As an illustration, we can mention the results obtained by the sweeping method when being used in taking population counts of *Therioaphis trifolii* and its parasites (DEBACH & SCHLINGER, 1964); sweeping gave about 66% accuracy with *Th. trifolii*, but only about 10% accuracy with the female parasites of the aphid; needless to say, data from such samplings could lead to completely misleading conclusions.

5. When using the stem counting method, we cut a certain number of plant stems in a given plot and take all the aphids present in these plants, including the aphid mummies. Some authors prefer to take only a certain part of the stems (FENTON & HOWELL, 1957). Living aphids may be shaken in a canister (GRAY & SCHUH, 1941) and taken to the laboratory for counting, or, as we have modified this method, the aphids can be shaken on a plastic dish of a light colour to distinguish them easily and then they are collected by a pincette and transferred into alcohol.

The stem-counting method, similar to the leaf-counting method, manifests a number of advantages when compared with other methods: (1) we can collect all the stages of aphids present on the stems, (2) it is relatively exact, (3) it can be also related to a certain plot; (4) it exhibits the same features during the whole season irrespective of plant conditions or weather; (5) it can be used practically in all the aphid species, (6) the material obtained is less in number and may be easily selected even when collected; (7) it may be used even in very low plants; (8) it covers also aphid mummies. There seems to be only one disadvantage, that we cannot collect parasite adults.

6. Leaf counting method. A certain number of leaves are collected as a sample unit.

As there are vertical differences among the leaves, leaves of different ages from different parts of plants are taken. For example, GEORGE (1957) took samples on one upper, one middle and one lower leaf from each 50 Brassica plants. SHANDS *et al.* (1965) examined 100 or more randomly located plants or sets of leaves each in a number of locations; either all the foliage or only three compound leaves per plant, which were located at random on each plant within the top, middle and bottom thirds, were examined. Similarly, BARNES (1960) took all aphids from 30 alfalfa leaves at the top, middle and bottom parts at 10 points in each experimental field, 300 leaves altogether per field, when sampling *Therioaphis trifolii* and its parasite populations; more counts were made when the aphid population was low. SLUSS (1967, SLUSS & HAGEN, 1966) divided the walnut leaves into three categories, i.e. new, mature and senescent leaves when counting populations of *Chromaphys juglandicola* and its parasites.

7. When using the square method, a square of certain dimensions (square foot—STERN & V. D. BOSCH 1959) is taken as a sample unit and all the insects encountered are collected irrespective of the number of stems, etc., in the given square plot.

8. Air suction method. A special method has been developed by DIETRICK, SCHLINGER & V. D. BOSCH (1959) in using a powerful air-suction collector to take samples from a given plot. The collected material was later anaesthetized and selected in the laboratory. This method has a great advantage in being relatively rather quick and thus enabling us to obtain a large number of samples from various parts of the studied area in a rather short time.

9. Visual inspection is in no way an exact method. This is, however, a kind of field experience that enables the observer to get general but often useful records: we often observe in nature that a species is highly parasitized in a certain part of the season, although no further detailed study is made. Such information is rather valuable in later studies on population relations of host and parasite in detail. Into this group such records usually belong which we get occasionally during various field observations.

10. Individual samples usually have the aim to illustrate or complete to detailed level a certain other method used. For example, we can obtain a certain adequate material of mummified aphids when using the stem-counting method, but such a number is not sufficient for determining the degree of hyperparasitism; thus, we collect the mummies in an individual way in a given plot.

11. Moericke traps are commonly used to determine the flight dispersal of aphids. Consequently, alate aphids are collected in this way. In some cases, this method could help to recognize the dispersal and parasite population in a certain plot through passive dispersal of parasite developmental stages in parasitized alate aphids.

12. Caged populations. Some authors used caged populations of aphids to recognize the seasonal dynamics of host and parasite populations (WAVE & SHANDS, 1965 *etc.*). ARTHUR (1945) used this method when artificially introducing the parasites in a corn field; the cages were later removed and the parasitized aphids counted.

Caging of isolated aphid colonies seems to reveal some negative features such as preventing aphid and parasite dispersal, consequently, a percentage of parasitism may be higher than in uncaged populations, or superparasitism may occur more often (see SMITH 1966).

13. Special collecting methods must be used when dealing with counting aphid eggs deposited on twigs, branches, etc., or of aphids occurring on woody parts (bark, branches) of trees and shrubs. The collecting and counting of root aphids is also a special case.

None of the methods is fully suitable in different respects. For this reason, several

methods of taking samples are usually used, in order to acquire the most exact results as possible. For example, we can obtain good results by the stem-counting method with respect to host-parasite population densities or degree of parasitism, but the sweeping method or individual samples may help us in the research of parasite sex ratio, degree of hyperparasitism, etc.

In our opinion, the stem or leaf counting method seems to be the most suitable, the other methods having only an additional character.

—INSECTICIDAL CHECKS. Under certain circumstances, insecticides may be used to help us to study seasonal population changes by comparing the results obtained in plots where natural enemies were eliminated by insecticidal treatment with the untreated plots. This method was used by BARTLETT (1957) in coccids and their natural enemies; it could, however, be used in the aphids and their parasites as well, namely, natural enemy effect may be isolated from the effect of biotic factors.

—HOST PARASITE LABORATORY ECOSYSTEMS. Laboratory conditions permit us to recognize the isolated influence of various factors on host and parasite populations. MESSENGER & FORCE (1963) used a bioclimatic chamber within which precisely controlled conditions of temperature, humidity and light were maintained. Judging from the methods used by these authors, studies on laboratory host-parasite systems (*Therioaphis trifolii*—*Praon exoletum*) should be directed in the tree following ways:

1. Isolation studies. Isolated individuals of host and parasite are observed under various temperature, humidity and light conditions (physical factors) with respect to such characteristics as speed of development, rates of survival to maturity, and rates of reproduction.

2. Density effects. In these studies, we determine the influence of various host aphid densities upon parasite reproduction as well as the influence of a varying number of adult parasites on parasite reproduction.

3. Population studies. In these studies, we investigate the influence of various factors on aphid population alone, and aphid-parasite populations.

—PERCENTAGE OF PARASITISM. This in an aphid population can be determined by several methods, some of them, however, seem to be avoided as they can result in serious mistakes.

1. Dissecting of living aphids. This seems to be the best method of determining the percentage of parasitism. However, it has one disadvantage as it is rather time consuming. By dissecting the aphids, we get information on the occurrence of parasite larvae, while the eggs are usually found less exactly, thus, the percentage of parasitism must be considered a little higher than the results show based on the presence of parasite larvae.

Some authors used to dissect higher aphid instars as their dissection is easier and also they can be more easily selected from the collected material (e.g. SLUSS, 1967, and others). We know, however, that this method is not so correct as, first, the parasites prefer certain host instars, and, secondly, the percentage of occurrence of various aphid instars in a colony can change for various reasons.

Some authors, including ourselves, support the practice of taking a certain given number of aphids from population samples to dissect, disregarding the instar (EVENHUIS 1962, STARÝ 1962, etc.). This helps us to form a more detailed picture on the percentage of parasitism, the possible role of host specificity of parasites and the presence of different aphid instars included.

The aphids can be dissected in different physiological solutions just after being transferred from the field to the laboratory. However, time possibilities and other technical reasons often make this difficult if not impossible, especially when a greater number of samples are taken. According to our experience, it is advantageous to

put the collected living aphids into approximately 70% alcohol. This saves our time in the field. Such preserved material can be dissected later at the aphids, as well as the parasite larvae inside them are well fixed, become whitish and the parasite larvae can be easily distinguished from the host body content when the host is dissected.

2. Fixation of living aphids. HAZILTON (1929) used the following method to determine the percentage of parasitism of a sugar cane pest aphid species by chalcid parasites: the whole sample of aphids was put in chlorid-hy drate in benzol solution: after a few hours the aphids became quite transparent. This material was then examined under a binocular microscope and the parasitized aphids easily counted. According to HAZILTON he was able to examine about 100 aphids within 1-2 minutes.

3. Counting of mummies. Many authors, especially when determining the percentage of parasitism in *Lissonota lanigena* by the aphelinids, used to relate the number of mummified aphids to the total number of mummified plus living aphids (JANKE 1939, LIBENHARDT 1940, DOMINANTINI 1947, BORE 1952, etc.). This method was discussed by EVINOV (1962) and classified as not being a very precise one as we need information on the parasitism of still living aphids.

PIMENTEL (1961) used a similar method in host and parasite population counts on Brassica crops, the mummified aphids without emergence holes were calculated weekly. As no samples were taken from the observed colonies, these counts were the only possible ones to prevent population disturbance. GEORGE (1957) used a similar method on Brassica crops. This method is perhaps useful if we observe the development of living colonies of hosts, the course of parasitism and if we do not take any samples of the material.

Unless we deal therefore with living colonies, the counting of aphid mummies to determine the percentage of parasitism must be criticized in agreement with WAT (1966). According to this author, misleading conclusions on parasite efficiency are often obtained from the large proportion of parasitized aphids left after the dispersal of non-parasitized aphids. It is well known, that the aphids gradually emigrate (alate specimens) from the colonies leaving the immobile mummified aphids (both with or without an emergence hole) behind. We believe that the records based on the number of mummified aphids are useful at the level of field observation, which does not permit more exact information: if there are a quantity of mummified aphids in an aphid colony, there is no doubt that this colony is heavily parasitized, although the percentage of parasitism can be, say, only 50 instead of 90-100 as it might seem to be, due to the counting of only mummies; naturally, such a determination of the percentage of parasitism would be a basic mistake in population studies.

REFERENCES. 7, 10, 21, 23, 36, 37, 45, 48, 97, 110, 128, 130, 227-8, 246, 258, 259, 260, 280, 301, 312, 325, 341, 350, 420, 450, 473, 487, 497, 515, 590, 606, 754, 757, 824, 891, 906, 914, 1003, 1005, 1019, 1035-6, 1062, 1064, 1065, 1090, 1100, 1111, 1146, 1200, 1267, 1274, 1277-9, 1308, 1329

Ecosystem

NATURAL COMMUNITIES The interplay of physical and biological forces has resulted in the establishment of characteristic groups of plants and animals in all habitable areas of the world. These interacting systems, composed of all the living organisms and their non-living environment, in an area sufficiently large to permit the characteristic exchanges of energy and perpetuation of the component organisms, are called ecosystems. The living portion of the ecosystem is the community. Each

community maintains itself by adaptations that allow it to withstand adverse influences and to obtain its needs by exchange with the environment (CLARKE 1954, HUFFAKER & MESSENGER 1964).

The members of a community or biocenose exhibit various interrelations: there are different degrees of positive or antagonistic relations. However, as mentioned by CLARKE, mutual tolerance and beneficial interaction have brought about a certain degree of interaction within the group. Thus, a community is defined by CLARKE as a group of mutually adjusted plants and animals inhabiting a natural area.

Due to the interrelations among the community members a community manifests a certain defined structure. However, although the function of every organism is defined in a community, the degree of its role is dynamic. There occurs a typical and defined natural balance in a community, which is reached just by the mutual tolerance and beneficial interactions of the community participants. This quantitative relationship, termed as balance of nature, has been defined as the tendency of the population densities of all species in the same general area to maintain a more or less consistent numerical relation to each other, due to interactions between each other and between the physical environment (see: DOUTT & DEBACH 1964). As the responses of the various members of the community to the influence of physical factors are different, fluctuations are observed around a certain population equilibrium: some populations may be favoured, populations of other species may decrease due to the influence of identical physical conditions, etc. Because of the mechanism of a community, the less suitable state, which appeared in a community owing to the effect of physical factors on some of its members by decreasing or increasing the degree of influence, is changed to reach the defined equilibrium position.

Every community gradually reaches a certain state, a climax, which is the result of the best adaptation of community members to given conditions of environment. Consequently, we can recognize well developed and less developed communities, closed and open communities, respectively. As shown by HUFFAKER & MESSENGER (1964), evolution leads to the origin of new forms to fill new roles or to fill old ones more efficiently; thus there is a tendency towards increasing the biotic complexity of communities.

As we are all aware, the separate communities are generally not strictly separated from each other, certain transitory zones occur, the ecotones of which reveal peculiar features both as to the number and density of populations of various species.

— PARASITES AS MEMBERS OF FOOD CHAINS. Generally, as to its structure, a community is composed of various food chains, which represent phytophagous insects and their associated enemies that limit their numbers in a community. In addition, there are various organisms in a community that have a certain independent role and do not belong to any food chain (saprophagous organisms, etc.).

Aphids, as a group of phytophagous insects, represent a basic part of a food chain: a number of various natural enemies are associated with them. The main role of the natural enemies, similarly as in the case of other food chains, is to limit the host aphid number thus preventing outbreaks and causing heavy injury to the basic element of the community, the plant element. The natural enemies of aphids act as a whole, the separate groups are complementary in action. The aphidids, as a group of aphid parasites, represent one of the groups of the natural enemies of aphids.

— NATURAL BALANCE. Aphids as phytophagous insects are able to respond to favourable conditions of their host plants and to favourable physical conditions by rapid and intensive increase of the population number in a given community. Aphid outbreak may cause heavy injury to the host plant. Consequently, fluctuations in population equilibrium follow and they must be put to equilibrium position by the

mechanism of the community: natural enemies, including the aphidiids, act as the corresponding mechanisms of the community in reducing the aphid number to a certain level, preventing basic injury to the phytocenose, or plant component of the community, by the aphids; moreover, the aphid species themselves manifest intrinsic regulation in density-induced dispersal. The action of community mechanisms, being a reaction to a fluctuation in equilibrium due to aphid population increase, come into action somewhat later; consequently, another fluctuation follows as a result of their action before an equilibrium position is reached. The action of community mechanisms via natural enemies of aphids is specific; in some communities the aphids are attacked by parasites only after they have reached a certain population level, in other communities the parasites attack aphids just as soon as they emerge from the overwintering eggs (temperate zone).

— **COMMUNITY AND SPECIES.** We are well aware that a species can be a member of various communities. Widely specialized aphids are just a typical example. Moreover, community alternation, connected with host plant alternation is an obligatory feature of biology in dioecious aphid species. The parasites, contrary to aphids, are more habitat dependent, i.e. they depend on a certain kind of habitat in their distribution, although they can be members of various communities of the same or a similar kind.

The occurrence of aphids in different communities means that they fall under the influence of balance of these communities which is dependent on a given community. Consequently, an aphid species may have different population equilibrium positions in different habitats. In one habitat it can be abundant, in another one scarce (see: DOVIT & DEBACI 1964).

— **ENVIRONMENTAL FORCES OF NATURAL LIMITATION.** The interaction between host and parasite populations has been an object of research of many authors. Of these, NICHOLSON (1933) and THOMPSON (1934) represent the main opinions, the other authors being more or less in agreement with either the first or second. The general idea of NICHOLSON's theory is that the host produces a fixed number of progeny and the number of eggs laid by the parasite is dependent on host density. This means that when host density is high, the parasite density is high, and when the first one is low the second one is low too. THOMPSON's initial assumption is that both host and parasite lay a fixed number of eggs, thus the number of eggs laid by a parasite ♀ is unrelated to host density and a parasite ♀ lays a limited number of eggs amongst its hosts. Several authors (MILNE 1957, KLOMP 1958, VARLEY 1959, HUFFAKER & MESSENGER 1964) have discussed these opinions; both theories possess many positive and negative features, they are, however, more or less complete from certain points of view. We agree with HUFFAKER & MESSENGER that controverse opinions and even a dogmatic keeping of the role of density dependence has been an unfortunate conflict in population ecology, as both groups of factors i.e. density dependent and density independent factors, play a complex role, the degree of significance of the separate factors being different in different cases (see: below).

— *The factors.* There is one basic principle as to the mechanism of natural limitation in that the environment acts as a totality and the elements of this whole are in important, sometimes delicate, interaction (HUFFAKER & MESSENGER 1964).

The factors of the environment are of the following two groups (CLARKE 1957, HUFFAKER & MESSENGER 1964)

Density independent factors, or conditioning forces, occur and act irrespective of density of populations and were defined as environmental factors or agents which, uninfluenced by density, contribute to the setting or fixing of a framework of potential environmental capacity or affect interim population realization when

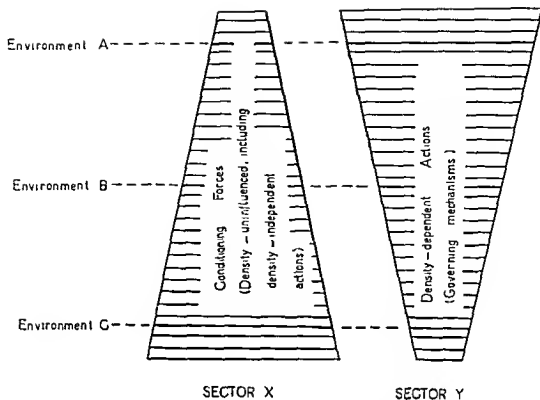


Fig. 292. Schematic representation relating the density-dependent and density-uninfluenced environmental forces of natural limitation to changes in population density under different types of environments. Relative widths of sector lines indicate relative correlation of corresponding forces with changes in population densities in time or in space. Sectors X and Y are considered together as parallel parameters.

Environment A: Physical factors continuously favourable; heterogeneous plant life; biotic factors predominate; natural enemies, food, suitable habitats numerous. Microhabitats spatially contiguous.

Environment B: Intermediate between A and C.

Environment C: Physical factors fluctuate excessively; intermittently favourable; plant life tends towards less complex stands, biotic factors, natural enemies, food, suitable habitats fewer, or not continuously present. Microhabitats more scattered, non-contiguous.

Sector X - conditioning forces (density-uninfluenced, including density-independent repressive actions) - climatic and edaphic conditions, light, protective places, quality and potential levels of food, conditions for existence of allies, direct competitors, parasites, predators, pathogens.

Sector Y - density-dependent (governing) actions: competition for food, shelter, breeding places, density-induced inhibitive reactions (HUFFAKER & MESSENGER, 1964).

capacity is not attained. The density independent group includes generally the physical features of the environments, mainly climatic, edaphic, and light conditions.

Density dependent factors, or governing mechanisms, were defined as actions or repressive environmental features, collectively or singly, which intensify as the population density increases, and relax as this density falls. This group of factors includes the biotic factors of the environment.

As mentioned above, these groups of factors are in interaction and their role can be different in different environments as shown by HUFFAKER & MESSENGER (1964) (Fig. 292).

In our opinion, the density dependent factors or governing mechanisms can be subdivided as follows:

1) Self-regulatory mechanisms of populations

A. Self-regulatory mechanisms of aphid populations

- (a) Intraspecific competition
- (b) Changes in daily fecundity rate
- (c) Dispersal

B. Self-regulatory mechanisms of natural enemy (parasite) populations

- (a) Intraspecific competition (superparasitism)
- (b) Changes in daily fecundity rate
- (c) Dispersal
- (d) Sex ratio (in biparental species)

2) Regulatory mechanisms of community

A. Regulatory mechanisms influencing the aphid population (action of natural enemies)

- (a) Cooperation
- (b) Competition
- (c) Displacement

B. Regulatory mechanisms influencing the natural enemy (parasite) population (action of hyperparasites).

In addition, we must stress again the complex action of these factors.

- *Aphid parasite populations.* There is a generally known developmental trend in the communities to reach a greater complexity. During the evolution of various communities, which is characterized by the interaction of their members with the abiotic environment and among themselves, various animal groups have obtained various roles in a community system. The aphidiid parasites have developed as parasites of aphids with the principal ecological role of limiting the number of their hosts, the aphids, within the frame of a given community.

- *Density dependence* - There is no doubt that the principal role of aphidids as parasites of aphids is density dependent. However, in the system of a community they only participate in the limitation of aphids; we know today that, on the one hand, each population of a community manifests a self-regulatory mechanism trying to limit its own numbers, on the other hand, the community developmental trend is directed to a greater complexity, the same role in a community being played by several groups of the community members which are capable of replacing each other in action with generally the same final results. The aphidids are just only one member of such groups so that they principally do not act in a separate way, but in dependence on the action of other members of the same ecological group, the natural enemies of aphids. Furthermore, the organisms that is limited, i.e. the aphids, and agents that limit the population number of aphids, are different organisms each of them reacting differently to the influence of environmental conditions, the latter including both the influence of abiotic factors as well as biotic factors such as host life history, microhabitat distribution, etc. It is obvious then that the occurrence and action of each of them must be limited to time and space, and the interrelations in action are clearly apparent - an equilibrium which is partially limited by the natural enemies must be limited during the whole season and in all the microhabitats in which it occurs in a community.

The above scheme is theoretical and the state mentioned would be ideal. Perhaps, a truly complete research of a virgin community in a climax state might show that it occurs in reality, too. However, various communities reveal different degrees of

completeness, so that the action of natural enemies is often found to be incomplete for many reasons.

Thus, concluding, the aphid parasites are principally density-dependent, they are only one of the agents which limit the density of the aphids in a community.

— Factors obscuring density dependence — 1. Different requirements of host and parasite on the environment. Aphids and parasites are two different groups, each of them showing its specific responses to the influence of the environment. Naturally, if they had to occur in the same community, they must be basically able to survive the influence of the factors under which the whole community has developed; however, they differ in detail very much. It is known that aphids and parasites exhibit different reactions to the influence of such factors as temperature, relative humidity, photoperiod, etc. For example, in a certain period of the season the aphid is capable of surviving high temperatures or high relative humidities, while the same conditions cause high mortality in the parasite population (MILLAN 1956, *Lysaphidius platensis*) or the parasites enter facultative quiescence (*Praon exoletum* in California, v. D. BOSCH et al. 1964, etc.). Similarly, the aphids generally start to develop under lower temperatures than the parasites and adverse weather conditions can cause changes in seasonal succession of host-parasite (PEAIRS & DAVIDSON, 1956, *Schizaphis graminum* and *Lysiphlebus testaceipes*). Moreover, the parasites respond differently to the influence of abiotic factors: during part of their life, for example during larval development, their response is determined by the response of the living parasitized aphid while in the adult stage the influence of the factors is a direct one. Similarly, it is known that the mortality is different in aphids and parasites during winter in the temperate zone, so that the number of parasites that emerge in spring may be considerably reduced in comparison with their density in the previous autumn (e.g. PAETZOLD & VATER, 1966, *Diaeretiella rapae*, etc.).

2. Self regulation is also an important mechanism which influences the population number of both aphid and parasite in a community. It is sometimes difficult to distinguish the period of influence of parasites as to the period of their true action from the effect of the self-regulatory mechanism in aphids, moreover, this dependence could be influenced by temperature.

3. Total aphid population density and population densities of different aphid species. Generally, increased host density is usually followed by increase of parasite density and increase of parasitization (SALT 1934), and any increase in the total aphid population should lead to an equal increase in parasitization in all aphid species. However, this is not the case, as the aphid species are not randomly mixed (PIMENTEL 1961) and, further, the aphids may or may not occur as a total aphid population with respect to parasite action. We have selected two extreme cases of communities to illustrate this:

In Brassica crops, as shown by PIMENTEL, three aphid species occur in N. America, *Brevicoryne brassicae*, *Lipaphis pseudobrassicae* and *Myzus persicae*. Thus with respect to the parasite action, they may be regarded as a total aphid population. The larger the total population, the larger the colonies and a likewise greater number of colonies are present. However, these colonies are not randomly mixed, and *Diaeretiella rapae* locates the more numerous and larger colonies more often, and a higher rate of parasitism results in these colonies. Thus, the parasitization of the separate species is not relatively equal, but the most abundant species is attacked most. Host preference, which undoubtedly occurs, is believed to play a role if equal choice is given to a parasite ♀.

As a small addition to the aforementioned, perhaps an extreme case as to its significance, is that cited by SCHLINGER & HALL (1960): *Lysiphlebus testaceipes* is a

common parasite of *Toxoptera aurantii* on Citrus in California. On Citrus, too, there is another common aphid, *Aphis spiraeola*, which is also attacked by the parasite, but the parasite is unable to complete its development, although the aphid is also killed. As we can assume, the parasite may be density dependent in action, keeping the two aphids as a single population, but a quantity of its progeny—that deposited in *A. spiraeola*—dies so that density dependence is unequal with respect to the parasite progeny emerging from *T. aurantii* and its further action. Still we should like to add that the parasite population that occurs in Cuba infests and develops successfully in both the aphid species mentioned.

Another example of total/partial aphid population is an alfalfa community (C. Europe). Three species of aphids occur, each of them being attacked by a separate complex of parasites, which have no relation to each other: *Acyrtosiphon pisum*—*Aphidius ervi*, *Praon dorsale*; *Therioaphis trifolii*—*Praon exoletum*; *Aphis craccivora*—*Lysiphlebus fabarum*, *Lipolexis gracilis*. Thus, with respect to parasites, each aphid represents a separate food chain. The situation is even more complicated as *Aphis craccivora* is only a temporary inhabitant of the crop.

There are quite a number of cases that are of an intermediate type where the parasite species exhibit a various specificity range in parasitizing aphid species in a community.

4. Host population density and host migration. Migration of host population from a certain community causes a more or less rapid decrease and often even a final lack of aphids in this community, while immigration to another community may result in an initial stage of population development or an increase of population if a certain population level occurred in such a community prior to immigration of a new population.

Both migration and immigration of aphids seems to obscure the density dependence of the parasites. Migration of aphids from a given community causes the decrease of the total aphid population present and this decrease may obscure the density dependence of parasites. Similarly, the immigration causes a rise in total population numbers. Furthermore, it depends on the host range of the parasites how they respond to the immigration or migration of their host (see above, and seasonal history).

A peculiar situation seems to exist in certain agroecosystems, in annual crops especially, where the aphids immigrate to a community in which there are no natural enemies (parasites) and the latter must later disperse to such places. Thus, dispersal of the parasites here plays a role as well.

Density of aphid population, besides the influence of host plant composition and photoperiod, is the factor inhibiting the production of alate aphids and later migration. We know (BONNEMAISON, 1948) that natural enemies (predators—author's note) because of feeding on aphid prey cause decrease of aphid numbers, thus being useful to aphids in reducing the interspecific competition in aphids and reducing self-regulation dispersal. Contrary to the predators, the parasites do not influence the self-regulatory mechanism of aphids. The parasitized aphids live relatively long before being killed by the parasite, and, being killed, they remain as mummies in the colony, so that even a high degree of parasitization means a decrease in the population of aphids only after a certain period. Only in few species, e.g. in some *Cinara* species (see: host and parasite relationship) the parasitized aphids leave the colony and are found separately on various parts of leaves, needles, etc., in such cases, a higher degree of parasitization could simultaneously mean the prevention or decrease in alate progeny production in aphids but even in this case, the aphids leave the colony just before being mummified, otherwise the presence of parasite larvae does not seem to change their behaviour.

5. Host range of parasite. Less specialized species of parasites are more dependent on the single host than the less specialized species, which may attack several hosts. Consequently, it seems that a closer density dependence relationship will occur in strictly specialized species. Narrow host range seems to be connected with the stability of the stand—a monophagous parasite could not survive in such places where the host could be temporarily absent. The dependence on host density in the widely specialized species may be obscured, on the one hand, by the non-random distribution of several host species, so that less numerous host populations are less attacked than the more numerous populations, although both the host species population may increase (see above); on the other hand, both migration and immigration of the host population from a given habitat may cause changes in density dependence (see above).

6. Other natural enemies. With respect to host-parasite density dependence this seems to be best apparent from the classification of the relations among the various groups of natural enemies: Natural enemies as a whole are primarily density dependent acting as agents of a community mechanism. They represent different groups of organisms, each of them exhibiting specific responses to the influences of environment both as to time and space. They replace each other in action, besides cooperation, even competition and displacement can occur.

7. Hyperparasites. They have the obvious primary role in limiting the number of primary parasites. However, their action is obscured by factors such as the relation between secondary and tertiary parasites, their own self-regulation, host range, etc. We know very little as yet about these phenomena.

8. Man's activity. This obscures the density dependence to a high degree. The agroecosystems, in general, are characterized by their artificial character (monocultures), which is controlled and supported by man; the complexity of the stand is much reduced in this way and the action of natural enemies (including parasites) becomes incomplete in many aspects. Agricultural practices, such as harvesting, may be highly unfavourable to host and parasite population conditions: mortality of either the host or parasite can be higher, migration being forced in consequence (see: v. D. BOSCH et al., 1966, *Acyrtosiphon pisum* and *Aphidius smithi*). Treatments reduce the host and parasite population to a different degree. When non-selective insecticide is applied, the subsequent immigration of new host aphid populations is more rapid than that of the parasite.

Selective insecticides reduce the host population and even the populations of various natural enemies to a different degree, unnatural relations among the natural enemy population appearing as a result (see: PIMENTEL, 1961, influence of insecticides on a Brassica community).

- Graphical representation - In a logarithmic scale of host and parasite population densities this apparently diminishes the fluctuation of parasite and host density relations, i.e. the percentage of parasitization. Vertical distance of the host and parasite population curves in a logarithmic scale gives directly the percentage of parasitization. Under constant percentage of parasitization the form of the curves must be fully identical, only the shifting to a vertical direction being different.

The percentage of parasitization is more apparent when host density and percentage of parasitization are plotted on a linear scale.

- Terms of population dynamics. Population dynamics of aphids and parasites may be classified in different terms.

- Short term dynamics - It covers the dynamics during one year. Most of the data obtainable in literature belong to this group.

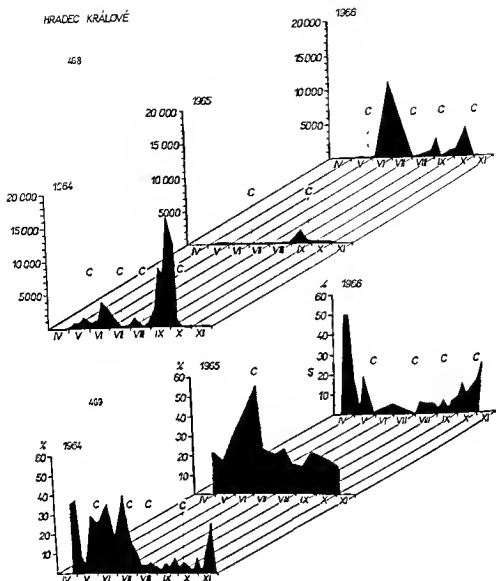


Fig. 293-294. Comparison of seasonal occurrence of *Acyrthosiphon pisum* and percentage of parasitization by *Aphidius ervi* in 1964, 1965, 1966, Czechoslovakia, Hradec Králové. 1964: dry and warm spring and summer, dry autumn. 1965: wet spring and summer, dry autumn. 1966: dry spring, wet summer, autumn normal; comparison with 50 years weather average C-cutting (nožák, in press.).

The following phases can be recognized in short term population dynamics (SMITH 1966):

1. Initiation is the period of establishment of the aphid population in the area together with its parasites, predators, pathogens and competitors. In short cycle agricultural crops and in other similar unstable environments, this initiation may require a new colonization of the area by at least a part of the complex. In other more permanent situations, the initial populations and their microdistribution (dispersion) are the end-product of differential attrition during a previous unfavourable period (winter cold, summer heat and dryness, etc.)

2. Increase is the period when conditions are most favourable to the aphids and without the intervention of outside factors (natural enemies, catastrophic weather or man), the aphid numbers would increase almost geometrically. In this period, the balance between the rate of reproduction of the aphids and the voracity of the aphidophagous species is most important.

3. Crash is the phase when the rapid rise of the aphid population is checked and the numbers are depressed to low levels or even exterminated locally. The depressing elements involved in overwhelming the aphid population begin to have their effects during the period of increase but now they assume a greater and more significant role. The depressing elements may act separately and a single element may be the critical one or several may operate together. The combinations of depressing elements vary from place to place and from year to year.

4. Survival during unfavourable periods.

— Long term dynamics — To understand the regularities in population dynamics the studies cannot be carried out only during one year as the population dynamics of species is connected with the previous year or years and this itself will exhibit a similar influence in the following year(s).

Every year conditions differ at least partially from each other and thus is obvious in the dynamics of host and parasite populations as well. This well known dependence can be illustrated by two examples:

The first example is several years research of alfalfa crop and population dynamics of *Acyrtosiphon pisum* and *Aplidiu crvi* in C. Europe (HOZÁK in press) (Figs. 293-294). It is obvious that dry weather in early spring supports the aphid occurrence (1964, 1966), while cold and rainy weather is unfavourable (1965). Parasites are effective in early spring, spring-summer and in late autumn.

The second example represents results of PIMENTEL's studies (1961) on population dynamics of Brassica infesting aphids and their parasites in Ithaca, N.Y. During the 1957 season, *Brevicoryne brassicae* was the most abundant aphid followed by *Myzus persicae*, while *Lipaphis pseudobrassicae* was least abundant. In 1958 the order of abundance was *M. persicae*, *L. pseudobrassicae*, *Br. brassicae* (Figs. 295-298). In both years, the heaviest parasitization in the aphid populations occurred late in the season, when aphid populations were most abundant.

— Area — Most of the studies deal only with a rather small part of the distribution area of host and parasite species. Most commonly, a plot in a field or other habitat is selected and the results are compared. Moreover, there is a lack of records on population dynamics on a wider scale, where the dispersal, etc., would be better apparent (see: WAY 1966).

— STABLE AND UNSTABLE ENVIRONMENTS. Virgin communities have arisen as the result of a long development during which the plants and animals tried to adapt themselves to the given conditions of the environments. Each community has tried to reach the climax state and we find various stages of this state in nature. It is known that complex communities are capable of defending themselves from various invaders. The complexity of stands is supported by their heterogeneity, the latter supporting a greater number of mechanisms preventing the equilibrium position from great fluctuations due to outbreaks of some species. However, although prevalent, mixed stands are not the only ones that can be found in nature. We have observed that in some places almost natural simple communities are found: extensive natural growths of the common reed, *Phragmites communis*, can be mentioned as an example.

PIMENTEL (1961) states correctly that tendency towards monocultures results in simpler populations, although the simplicity is only relative, in which the number of

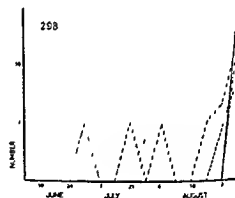
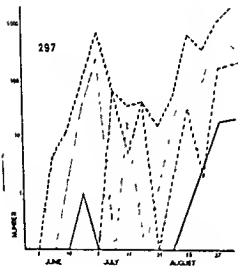
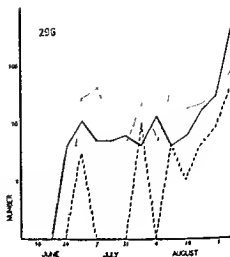
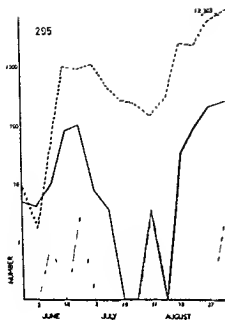


Fig. 295-296. Natural limitation of aphid populations on Brassica crops. The number (log) of *Brevicoryne brassicae* (—), *Myzus persicae* (---), and *Lipaphis pseudobrassicae* (-.-.) per 100 plants (PIMENTAL, 1961)
295: 1957, 296: 1958

Fig. 297. Natural limitation of aphid populations on Brassica crops. The number (log) of *Diuraphis rapae* (—), *Charips brassicae* (---), and *Aphis fletcheri* (-.-.) in *Brevicoryne brassicae* and number of *Psaron sp.* (—) in *Myzus persicae* per 100 plants during 1957 (PIMENTAL, 1961)

Fig. 298. Natural limitation of aphid populations on Brassica crops. The number (log) of *Diuraphis rapae* (—) and *Charips brassicae* (---) in *Brevicoryne brassicae* and *Diuraphis rapae* (—), *Charips brassicae* and *Lipaphis pseudobrassicae* (-.-.) in *Myzus persicae* per 100 plants during 1958 (PIMENTAL, 1961)

species is considerably less, the lengths of the food chains are considerably shortened, and large amounts of food are readily available for exploitation. The following examples will give an illustration of this:

Hyalopterus pruni occurs in various numbers on wild *Prunus* species in deciduous shrubs and forests. It has been attacked by a number of parasite and predatory species almost from the beginning of its occurrence, as the enemies overwinter in such mixed stands and other alternative hosts as well. However, another situation occurs when the aphid emigrates from such mixed stands and immigrates to *Phragmites communis* growth. In reeds, there are no other aphids and consequently the natural enemies (parasites) must disperse there from the neighbouring communities. This gives a possibility to the aphid, under favourable conditions, to reach high population levels before the natural enemies become significant as can be commonly seen in nature.

Aphis fabae occurs on *Euonymus europaea* on the edges of deciduous forests in spring, where it is limited by various natural enemies, including parasites. In the late spring, it migrates from this habitat and immigrates to steppe type habitats. Here we can see the difference according to the type of stand into which the aphid had immigrated: in mixed natural or semi-natural stands such as roadsides, waste places, etc., the aphid is soon parasitized, as parasites, such as *Lysiphlebus fabarum* or *Lipolexis gracilis* have occurred in these places from early spring and here attack various other aphids; thus, *A. fabae* immigrates to such places and is attacked in a similar way as the other species. However, in simple stands, in sugar beet fields, the stand is an annual crop, so that neither aphids nor parasites can be found there in early spring as they did not overwinter here; thus, *A. fabae*, when immigrating to such stands, is not limited by any biotic agent and may soon reach outbreak numbers; the natural enemies, including parasites, must disperse to such places from the neighbouring habitats. It is well known that in these places the aphid is parasitized first at the edges of fields, which are near roadsides, etc. (see: foci).

— *Diversity of stand.* As mentioned earlier, a defined equilibrium position is typical for every community. Fluctuations around this equilibrium occur due to the different effects of the environmental factors on the populations of the separate members of the community. Community mechanisms act through various agents, one of which are the natural enemies. As mentioned by FRANZ (1961), cooperation occurs among the natural enemies in a community, one aspect of it being the complementary action of natural enemies; this may involve a time component—if one of the natural enemies is lacking, the other replaces it in space and dispersion—host individuals which are not found by one natural enemy will be detected by another one (see: interspecific relations). It is apparent from this kind of community mechanism that the more agents occur in a community, the more accurate will be the limitation of a phytophagous species in this community, consequently, a better balance occurs in heterogeneous communities.

— *Density of populations.* The fact has been observed and confirmed by many authors that in mixed stands the number of species is higher, but their populations are relatively lower, while in the simple stands the number of species is less, but their populations are higher.

In aphids and parasites, the mentioned dependence may be confirmed by extensive field observations. PIMENTEL (1961) proved this dependence by the research of Brassica crops grown in mixed and simple stands. Simple stands were those where *Brassica oleracea* was exclusively grown, while mixed stands contained also wild Cruciferae. In 1957, the significantly greater number of parasites present in the single species planting as compared with the number found in the mixed species planting

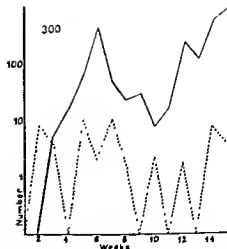
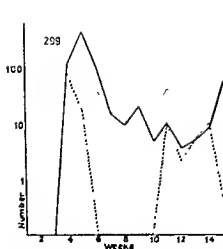


Fig. 299. The log number of aphids per unit plant area in the mixed (---), single (—), and sparse-single-species (...) stands during the 1958 season. *Brassica oleracea*, Ithaca, U.S.A. (PIMENTEL, 1961).

Fig. 300. The log number of parasites per unit plant area in the mixed (---) and single-species (—) stands during 1957. *Brassica oleracea*-plant, *Brevicoryne brassicae* (mostly)-aphid. Ithaca, U.S.A. (PIMENTEL, 1961).

was directly related to the high *Brevicoryne brassicae* population in the latter. As the parasite population also increased on the aphid population, the ratio of parasites to aphids was larger in the single species plot than in the mixed, 18.9% to 8.1% respectively. These parasite trends were not apparent in 1958, mostly due to the change in number of *Br. brassicae* from an outbreak level in 1957 to a markedly lower level in 1958 (Figs. 299, 300).

- *Species diversity and outbreaks.* PIMENTEL (1961) briefly reviewed the opinions of different authors on outbreaks and separated them into two groups: one group of workers, due to evidence supporting the proposition that more outbreaks occur in a single species stand under man's cultivation than in natural mixed species communities, believes that in virgin forests outbreaks never occur. According to another group of authors, on the contrary, outbreaks are not restricted to cultivated areas, but occur occasionally in the virgin forests. Nevertheless, authors of both groups agree that outbreaks are most frequent in cultivated areas.

With respect to literary records on aphid outbreaks as well as to our own observations, aphid outbreaks may be observed in virgin stands, semi-natural stands and cultivated stands, being most common in cultivated stands. For example, *Phyllaphis fagi* is known to often occur in outbreak numbers in virgin beech forests in the Carpathian mountains in C. Europe as well as in parks. Various aphid outbreaks may often be observed on various ornamentals in parks (*Aphis fabae*) on *Philadelphus coronarius*, *A. spiraeifolia* on *Spiraea* sp., in C. Europe. Cultivated crops, naturally, exhibit the greatest number of various examples. *Aphis fabae* on sugar beet, *Schizaphis graminum* on cereals, *Rhopalosiphum maidis* on maize, *Toxoptera aurantii* and *Aphis spiraeicola* on Citrus, etc.

- *Multilateral limitation concept* The complex action of natural enemies in nature means, in addition to others, that a host is theoretically attacked and limited by natural enemies in all the environments in which it occurs. This has been clearly shown by FRANZ (1961)

With respect to our multilateral control concept we must admit that there is no doubt that a state similar to the state recommended as ideal or at least dealt with in (aphid) control is more or less achieved in nature, with no dependence on man. In connection with the nomenclature used, we have to distinguish such a state existing with and without the interference of man. For this reason, we propose using the expression "multilateral limitation" in a similar way as we use the terms "limitation" and "control" as proposed by FRANZ (1961). As to the definition of multilateral limitation, it seems possible to classify it as a result of complementary action of natural enemies in nature without the interference of man.

- *Clean culture concept.* We have shown above that diversity of stand supports its stability. However, contrary to these opinions, PEAIRS (1947) recommends the application of a so called "clean culture concept", which means the general destruction of weeds and hedgerows in the neighbourhood of crop field.

PEAIRS's concept was put under question by PIMENTEL (1961), who stressed the role of hedgerows and weed plants in providing the additional diversity of crop fields and thus increasing the stability of the latter stands.

As we have shown in the chapter on parasite foci, we must distinguish and select the dominant plants that occur in hedges or as weeds in a parasite conservation program. With respect to our classification of foci, there is no doubt that many habitats such as hedgerows or weed plant growths represent valuable foci of parasites of pest aphids; these parasites kill the pests that immigrate into such places, the parasites may disperse from there to the cultivated crop neighbourhood, they may hibernate there, etc. On the other hand, there may be also parasite species present in such habitats that exhibit no close relationship to the neighbourhood. Thus we must classify such habitats prior to their evaluation. Moreover, the aphids present in such habitats can be indifferent with respect to parasites, but valuable as to the predators.

There is no doubt that crops are artificial in their monoculture character; just this character is required by man and this cannot be changed, although monocultures are known as a part of the environment favourable to pest outbreaks. Thus, preservation of at least small mixed stands in cultivated areas seems to be recommendable.

- *Annual and perennial crops.* Agroecosystems may be associated with annual, biennial or perennial crops. Although all these ecosystems exhibit the basic features of agroecosystems, there are differences among them with respect to the stability.

Annual crops seem to be the least stable: each year seed is grown in a new plot and the development of a community starts, various species immigrate to this area from the neighbouring communities. At the end of the season, or even earlier, the community is practically destroyed by harvest and ploughing.

The next year, a similar community develops in another plot in a similar way. Cereals, vegetables, potatoes and other crops are examples.

Perennial crops exhibit the character of an annual crop during the first year of their existence, when the community starts to develop. However, contrary to annual crops, perennial crops are grown on the very same plot for several years, therefore the community is not destroyed by ploughing at the end of each year. Alfalfa crops, or orchards, may be mentioned as examples.

It is obvious from these features of annual and perennial communities that perennial communities develop a better stability than the annual crops.

- *Life history of aphids.* Aphids migrate and immigrate to various communities during the season. If they migrate inside various communities of a given type of habitat (forest or steppe-field), their immigration exhibits features of commonly occurring dispersive movements in a similar way to other members of the community. However, a certain part of the aphids, the dioecious species in the temperate

zone and subtropical zone, have habitat alternation as an obligatory part of their life cycle: consequently, the aphids migrate from one habitat, in which they are thus absent for a certain period, and migrate to another habitat, in which they were not present earlier and they again leave it later in the season and return to the original first habitat (scheme: forest – steppe – forest). This type of immigration and migration causes great fluctuations around the equilibrium position in corresponding communities: natural enemies, including parasites, must attack other hosts in case of a given host emigration, or, vice versa, they must attack and limit the number of a newly immigrant host population.

– *Host specificity of parasites.* Generally, the parasites act as one of the agents of the community to limit the population number of a given host species. This dependence is better apparent in strictly specialized parasites, if several host species are present in a community, the parasite attacks the most numerous population. This fact was well documented by RIMENYIL (1961). In widely specialized parasites there is an important feature as to whether several host species are present in a given community; otherwise the parasite acts as a strictly specialized species as it cannot realize its host range. For example, *Praon volucre* and *Ephedrus plagiator* attack the following aphids in plum orchards in C. Europe: *Hyalopterus pruni*, *Phorodon humuli*, *Brachycaudus cardui* and other aphids in the orchard neighbourhood; however, when *H. pruni* occurs on reeds, this growth is practically a natural simple stand where the parasites do not find another host species. Similarly, when a widely specialized parasite species is introduced to control a host species in a new country, its range of specificity is artificially restricted as other host species do not occur in the new environments (*Chromaphis juglandicola* – *Trioxys pallidus*, in California).

distributed in the same kind of habitat, but each of them requires certain micro-habitat conditions of temperature and relative humidity (see: V. D. BOSCH 1956, 1957, etc.). *Myzus persicae* and its parasites in greenhouses: *Ephedrus persicae* attacked the aphid only on exposed parts of the plants, while *Aphidius matricariae* preferred shady situations (MCLEOD 1937). In the mentioned cases, it is apparent how one parasite species is replaced by another one in a certain microhabitat (*Therioaphis trifolii*, *Myzus persicae*) or not (*Schizaphis graminum*). If the parasite is not replaced by another parasite species, it is expected that another natural enemy will come into action.

— *Man's influence.* Man's influence on various communities is generally known and can vary from being almost negligible (virgin lands) to entire devastation. Agroecosystems have developed as a result of the growing of certain crops by man and attachment of various animal (and plant) species to these crops.

All these degrees of man's influence on the communities are connected with changes in the stability of these communities: man's influence causes changes in the populations of animals through changes in plant composition, the population equilibrium of animal species changes as well and the whole community is strongly influenced. In many cases, original natural communities were exterminated and secondary communities have developed instead in many places.

Man's influence on the community stability seems to be best apparent in the comparison of virgin lands and cultivated lands occurring at the very same places after cultivating the virgin land. Or, agroecosystems themselves, as they are more simple as to their structure, may be used: growing of crops by man in areas far from their native home caused that the composition of a community associated with a given crop varies depending on area. Agricultural practices, such as harvesting or ploughing, the whole crop rotation system, they all have a great influence on community stability. Changes in physical environment, such as irrigation, strongly affect the composition and fluctuation in agrocenoses. Chemical treatments cause a disturbance in a treated community either of a rather general type in the case of complex non-selective treatment, or partial in the case of selective insecticide application. Growing of resistant varieties eliminated also certain groups from the community associated with a certain crop. Finally, new members of communities are introduced, either accidentally or purposefully, by man.

— *SYNECOLOGICAL OPTIMUM.* According to FRANZ (1964), if we plot the distribution of enemies (Fig. 301) above the zonation of the more basic conditions, we obtain a pattern which elucidates why outbreaks (gradations) occur. In fact, they are often limited to zones that are free from effective natural enemies even if other conditions are suboptimum. The term synecological optimum, coined by RUMTSOV (1937) seems to very well describe the situation. This scheme seems to apply to the case when a pest aphid spreads to new areas, where it is not attacked by effective natural enemies. *Therioaphis trifolii*, at least in the initial stages of its spread in California, might be mentioned as an example. In other cases, such as many *Aphis* species that are cosmopolitan in distribution, the aphid may spread from the area in which it is limited by a certain parasite, but it can spread into another area where members of another parasite faunistic complex are distributed and adapt themselves to parasitization on the new immigrant; the latter process is common in nature as we have observed in such cases as *Toxoptera aurantii*, *Aphis spiraeicola*, and others. However, it is a question whether an area where the aphid (phytophagous insect) is free from an effective natural enemy may be defined as the synecological optimum. When the aphid is not limited by the action of natural enemies in a community, other conditions being favourable, the aphid reproduces and reaches outbreak numbers in consequence; in the latter case, however, the aphid destroys the host plant supply

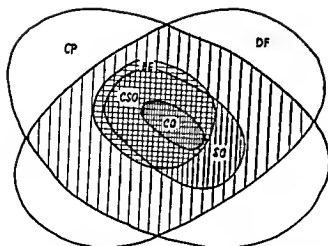


Fig. 301. Synecological optimum determined by the imperfect coincidence of the host's and its effective enemy's zone of distribution. CP – climatic potential distribution, area of monophagous plant feeding insect; DF – distribution of food plant; CO – climatic optimum zone; CSO – climatic suboptimum zone; EE – effective enemy zone; SO – synecological optimum for phytophage (FRANZ, 1964).

and there are (for a certain period) no environmental biotic forces that could limit such an aphid population fluctuation. It is known that natural enemies are considered just to be favourable for an aphid species in preventing such a situation. Thus, according to our opinion, the synecological optimum expression would be more suitable for a contrary situation, i.e. if the aphid occurs in a well balanced community, where its population fluctuations are limited around equilibrium position. Synecological optimum for a phytophagous species does not seem to be in a community which has become disturbed due to the immigration and occurrence of a new member, but in a well balanced community, irrespective of climatic optimum or suboptimum zone. The evolution of communities, which try to reach a climax stage, seems to be the best proof.

– ZONES. Natural communities that occur today in separate climatic zones are results of adaptation of certain groups of organisms to the conditions of these zones. Thus, they will exhibit the same basic features of a community, i.e. there occurs a balance, and populations have a certain equilibrium position of population of separate species. The peculiarities of the separate zones have naturally influenced both the evolution and dynamics of the communities: seasonal fluctuations of aphid and parasite populations are different in the temperate zone, the subtropics, the tropics, and also in greenhouses.

Hard winter and hot summer conditions have a marked effect on the dynamics of community members in the temperate zone. Winter is spent in quiescent states, spring and autumn conditions are favourable to the dynamics of many communities while hot summer conditions are mostly connected with a decrease of population numbers, on the other hand, hot conditions occurring in summer are favourable for other species.

In the subtropics, hot summer conditions seem to be generally unfavourable, while the rest of the year is characterized by apparent fluctuations in population numbers. In the tropics, the dry and rainy season seems to have both positive and adverse effects on the dynamics of aphid and parasite populations.

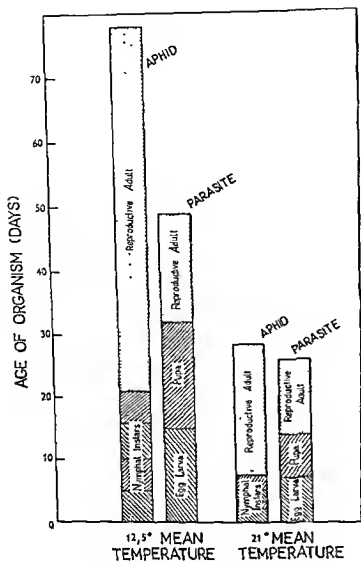


Fig. 302. Host-parasite system: *Therioaphis trifolii* - *Praon exoletum* (= *palitans*). Histograms showing relative durations of development and reproduction for the aphid *Th. trifolii* and its parasite *Pr. exoletum* when reared in 2 different fluctuating temperature environments with means of 12.5 and 21°C, resp. 40 replicates used for aphid life cycles and for parasite development; 20 replicates for parasite reproduction. Age intervals based on median response times (MESSENGER & FORCE, 1963).

In a greenhouse (temperate zone), changes in temperature due to yearly seasons (artificial heating in winter, mild conditions in spring and autumn, and high temperatures in summer) significantly influence fluctuations in host and parasite populations present.

Thus, in general, we can recognize the same basic features of natural limitation of aphids by parasites in separate climatic zones; as to the structure, in all the communities in all the zones the parasites are only a part of certain aphid-natural enemies food chain; as to their role in the communities, their significance can be high or low in a general way, differing in dependence on season, year, etc. Thus, it is not possible to say that the parasites are more or less effective in a certain zone, their role is specific both with respect to a given host and community. Although natural commu-

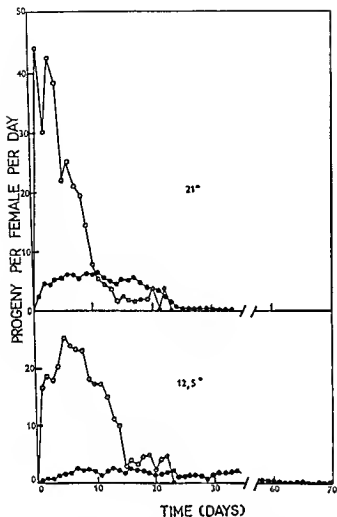


Fig. 303. Host-parasite system: *Therioaphis trifolii* - *Praon exoletum* (= *palians*). Daily reproductive pattern during adult life for *Th. trifolii* (solid circles) and *Pr. exoletum* (open circles) reared in 2 different fluctuating temperature environments. 40 replicates for the aphid; 20 replicates for the parasite (MESSENGER & FORCE, 1963).

nities have developed depending on separate climatic zones, the agrocenoses or communities of cultivated crops may often be found today in different climatic cones or at least their parts irrespective of their origin, and, consequently, their associated fauna and its dynamics is different and depends on a given zone.

EXPERIMENTAL COMMUNITIES. The influence of environmental conditions on the populations of host and parasite in various natural communities is of a complex character in nature and we cannot separate the influence of separate factors there in an isolated way. Laboratory conditions, on the contrary, allow us to deal with the influence of separate factors and to recognize the true action of at least some of the complicated mechanisms of the community. We have intentionally separated the experimental communities as they represent an artificial system due to the isolation of separate factors that never can be met with in nature.

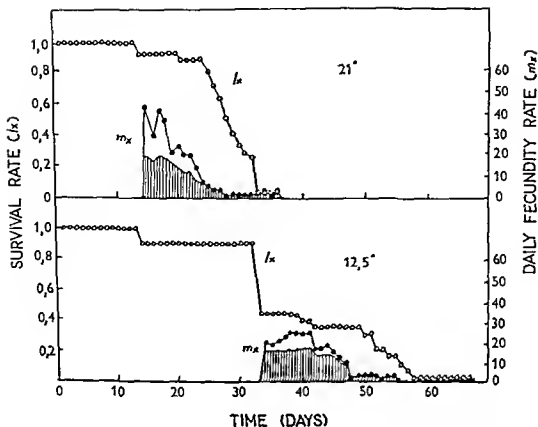


Fig. 304. Graphic representations of life tables for *Praon exoletum* (= *palitans*) reared in 2 different fluctuating temperature environments with means of 12.5 and 21°C. Time is measured from oviposition of the egg; I_x curves (open circles) show the proportion of the initial sample still alive at the indicated times; m_x curves (solid circles) show the mean daily reproduction rates for adult parasites, based on total eggs produced per day; shaded areas under the m_x curves show the number of effective eggs (equivalent to number of hosts parasitized) laid per day (MESSENGER, 1964).

Many authors have dealt with the laboratory studies of host and parasite populations. However, most of such studies cover only the influence of some factors and thus the experimental communities are classified rather incompletely. There are only several papers which include really comprehensive data, such as HAFEZ (1961), PIMENTEL & AL-HAFIDH (1963), MESSENGER & FORCE (1963), MESSENGER (1964), BROUSSAL (1966).

In host-parasite experimental community studies, we support the approach of MESSENGER & FORCE who stress the difference of host and parasite as organisms, which exhibit specific features and may be influenced by identical environmental conditions to a different degree. Thus, in such studies, it seems to be best to deal first with the influence of separate factors on the isolated populations of host and parasite, then population density dependence and finally with the general population studies. In certain aspects, naturally, we cannot separate the host and parasite populations completely as the aphidiids are parasitic organisms during a certain period of their life, thus, during the larval development we can deal only with the influence of factors on the parasite through the host aphid, while in the adult stage we can recognize the real direct influence of various factors on parasite adults.

There is no doubt that the research of experimental communities represents an

Factor	<i>T. maculata</i>	<i>P. palitans</i>
Climate	+	+
temperature	+	+
humidity	+	+
photoperiod	o	+
light intensity	+	+
wind velocity	+	+
evaporation rate	+	+
Food	+	+
Biotic		
diapause	o	+
crowding	+	+
mating	o	+
sex ratio	o	+
fertility	o	+
superparasitism	o	+
oviposition rate	+	+
host size	o	+
host stage	o	+

Table 14. Various kinds of environmental and biological factors that have been found to influence the innate capacity for increase (r_m) of *Therioaphis trifolii* (= *maculata*) and *Praon exoletum* (= *palitans*) (MESSENGER, 1964).

extensive field, where further studies are urgent and recommended. There is a necessity for studies on self-regulatory mechanisms of host and parasite populations (intraspecific competition, dispersal, etc.), on the interrelations among natural enemies, on the influence of hyperparasites, etc.

- ISOLATION STUDIES. The research on the influence of separate factors, both abiotic and biotic ones, revealed that some of them influence only either the host or parasite, while others exhibit the influence on both the groups of organisms; furthermore, the latter influence differs with respect to host and parasite. *Therioaphis trifolii* and its parasite *Praon exoletum* may be used as an example (MESSENGER & FORCE, 1963, MESSENGER 1964) (Figs. 302-304, table 14).

- DENSITY EFFECTS. Results of studies of various authors agree that host density influences parasite density to a certain extent, which depends on the specific features of a given parasite.

When gradually higher host densities were exposed to an isolated parasite ♀, the daily fecundity rate increased up to a certain limit, over which the increase in host numbers had no effect on the rate of parasitization (Fig. 305). This dependence of daily fecundity rates of an isolated parasite ♀ may be obscured by the influence of such factors as the interval of host presence or absence, age of the ♀, mating, photoperiod, temperature, intrinsic features of populations, etc., as shown by HAFEZ (1961) in *Brevicoryne brassicae* and *Diaeretiella rapae*, MESSENGER & FORCE (1963) in *Therioaphis trifolii* - *Praon exoletum*, BROUSSAL (1966) in *Brevicoryne brassicae* - *Diaeretiella rapae*. Further, in host and parasite populations, the density of parasites influences the daily fecundity rate of separate parasite ♀♀ as well (see below, population studies).

Similarly, the total fecundity rate is specific for a parasite (potential fecundity), it may be fully realized under favourable conditions (realized fecundity), one of which represents the host density, but it has a certain specific upper limit, which depends on the parasite species, over which it cannot increase although host density may further increase.

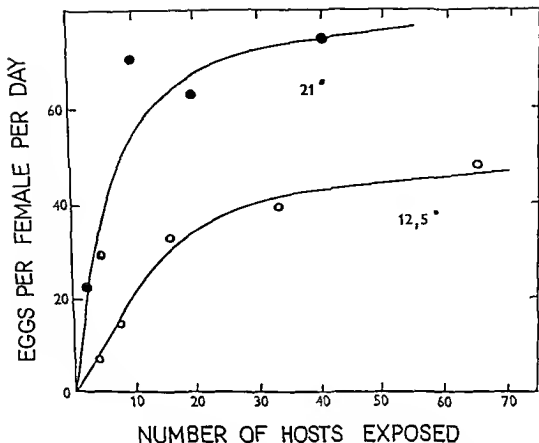


Fig. 305. Host-parasite system: *Therioaphis trifolii* - *Praon exoletum* (= *palitans*). Effects of varying host densities on parasites daily fecundity rates, where the indicated numbers of 3rd and 4th instar *Th. trifolii* nymphs were exposed for 24 hrs to isolated *Pr. exoletum* ♀♀. 4-5 replicates at each host density. Open circles, 12.5°C mean temperature; solid circles, 21°C mean temperature (MESSENGER & FORCE, 1963).

- POPULATION STUDIES. In population studies, to understand the significance of parasites in such systems, it is necessary to deal first with the development of the aphid population alone, then with host and parasite population relations, and then with population of the parasite.

1. An aphid population itself, with no parasites present, gradually increases until it reaches a certain density under which much of the food plant is destroyed. Then the decline of the population takes place as a consequence of the shortage of food. This is an apparent self-regulation of aphid population in this system: population must decrease otherwise the food source would be destroyed basically and the whole population would become extinct. Under natural conditions, dispersal possibility exists, which does not take place in laboratory conditions. This dependence of aphid population on the conditions of the food plant was well documented by PIMENTEL (1961): *Brevicoryne brassicae* population increased slowly for the first three weeks and by the 4th week reached a maximum density of 8,953. The subsequent decline in the aphid population was attributed to the aphid which destroyed much of its food plant. This decline halted at the 12th week when the aphid density was about 3,000. Approximately 3,500 aphids appeared to be the density level at which the supply of plant food balanced aphid demand for it. Thus, intraspecific competition limited aphid numbers in the system (Fig. 306).

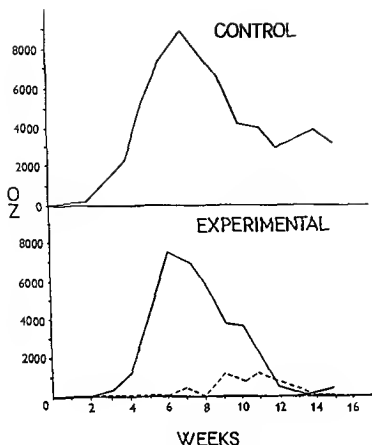


Fig. 306. Upper graph: the control aphid population (—) in the 16-cell population cage. Lower graph: the experimental braconid parasite (---) and aphid host (—) in the 16-cell population cage (PIMENTEL & AL-HAITHI, 1963).

2. In an aphid and parasite population system, the parasite population increases slowly and the parasites affect the aphid population after it reaches a certain level.

PIMENTEL, in an experimental population of *Brevicoryne brassicae* and *Diaeretiella rapae*, found that this population behaved in a similar manner to the aphid population alone (see above, aphid population), the parasite population increased slowly and apparently did not affect the experimental aphid population until the aphid numbers declined to about 4,000. Then a sufficient number of parasites existed to force a significant decline in the aphid population. A low level was reached in the 14th week and following this the aphid population again started to increase. It is obvious that in this system the parasite was unable to reduce the aphid except when it was reduced severely by the shortage of food (Fig. 306).

In a *Therioaphis trifolii* and *Praon exoletum* system (MESSENGER & FORCE, 1963), where there was no shortage of food as new plants were continually added, the parasite was, under certain conditions, responsible for the decline of the aphid population after it had reached a certain level, temperature influenced the parasite significance. In lower temperature conditions, aphid numbers rose in a manner somewhat similar to the control aphid population system, but the increase was more variable, parasite reproduction causing a larger or smaller lag in aphid rate of increase; thus, under

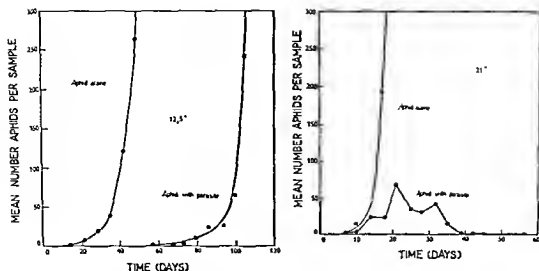


Fig. 307. Host-parasite system: *Therioaphis trifolii* - *Praon exoletum* (= *palutans*). *Th. trifolii* population growth curves when reared on seedling alfalfa plants in a fluctuating temperature environment averaging: left - 12.5°C, both free and in the presence of *Pr. exoletum*. Population density counts based on mean number of aphids of all stages occurring in samples of 54 trifoliate leaves each. Right: ditto, averaging 21°C both free of and in the presence of *Pr. exoletum* (MESSENGER & FORCE, 1963).

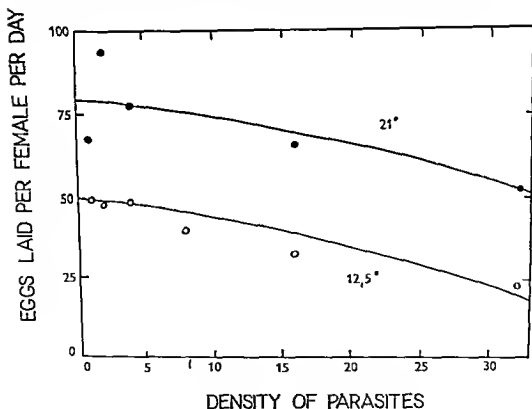


Fig. 308. Host-parasite system: *Therioaphis trifolii* - *Praon exoletum* (= *palutans*). Effects of varying parasite densities on parasite daily fecundity rates, where 80 third and 4th instar *Th. trifolii* nymphs were exposed for 24 hr to the identical numbers of *Pr. exoletum* ♀♀. 4-5 replicates at each parasite density. Open circles, 12.5°C mean temperature; solid circles, 21°C mean temperature (MESSENGER & FORCE, 1963).

these conditions, the parasites were unable to check the growth of aphid population, although they were gradually increasing in number. In this case, eventual termination of aphid population increase would be the shortage of food. On the contrary, in higher temperature conditions, there was a clear termination of aphid increase well below the plant carrying capacity, followed by declines to low levels (Figs. 307, 308).

3. Parasite population manifests similar self-regulation as the control aphid population. Unfortunately, we cannot separate the control parasite population as it must be connected with the host population. However, the self-regulation of the parasite population is apparent in changes of parasite daily fecundity rates due to parasite density. MESSENGER & FORCE showed clearly that the higher density of parasites the lower is the daily fecundity rate of a parasite ♀. Thus besides dispersal, which was prevented under laboratory conditions, the self-regulation mechanism of a parasite population seems to be in reducing the daily fecundity rate of separate ♀♀ and in increasing superparasitism, i.e. intraspecific competition. Apparently, dispersal of parasites should prevent such a state in nature. WAY (1966) showed that in systems of *Brevicoryne brassicae* and *Diaeretiella rapae* the host was quickly eliminated when parasite dispersal was prevented but when dispersing aphids and parasites were removed, an oscillating host population was maintained for over 300 days. Sex ratio seems to have a similar role, being also influenced by host and parasite density relations.

Parasite Effectiveness

Effectiveness of parasites (natural enemies) has been classified by a number of different authors. Perhaps the best definition is given by V. D. BOSCH & TELFORD (1964). These authors believe effectiveness (efficacy) to be determined by the environment, its physical and biological properties as well as its stability and relative permanence. We deeply support this stressing of the role of environment with respect to parasite effectiveness. However, in our opinion, the intrinsic features of the parasite are omitted in the definition mentioned above: even a most favourable environment cannot cause an increase in parasite effectiveness if the intrinsic features of the parasite, its potential rate of increase, is low. Thus, we should perhaps complete the above definition by adding the significance of the intrinsic features of the parasite species, as follows: parasite effectiveness is a result of the interaction of the intrinsic features of the parasite species with the environment, its physical and biological properties as well as its stability and relative permanence.

In nature, the parasite acts as an agent of community mechanism to limit the population number of aphids to a given equilibrium. However, we must stress that the population equilibrium of aphids in a given community exists naturally irrespective of man's interest. Some fluctuations in aphid numbers can be higher, some lower, but, in natural communities at least, each fluctuation of the aphid population is decreased by the action of certain mechanisms, both self-regulatory and/or community mechanisms. However, if the fluctuation of an aphid population causes significant damage to crops, man is inclined to believe that the natural mechanisms are ineffective, although such fluctuations occur in nature. Man has a subjective viewpoint in classifying the natural enemies (parasites) according to whether they are able to protect his crop from damage or not, disregarding the community. This is natural as man tries to harvest as much as he can and he is not inclined to let an extensive part of his crop be consumed by insects due to fluctuations in a community. First, man has tried to eradicate the pests in his crops by chemicals and other control

measures. We know today that this trend is incorrect: we cannot eradicate the insects, they are a part of the environment and we must leave them to take a certain part of our harvest. Thus, a compromise has appeared in an integrated control trend (see: integrated control chapter). The insect populations are studied, their population equilibrium is established; man has stated a certain economic threshold over which he tries to prevent the pests from reproducing, but otherwise the mechanisms regulating the natural limitation of pests (aphids) are left as untouched as possible. It seems, at the present at least, that as man is responsible for the existence of agroecosystems, which are simple stands at most where the natural balance is more difficult to preserve, he must help to reduce some kinds of fluctuations in population numbers that occur because of this state of crop communities.

The parasite effectiveness must be considered also with respect to the kind of damage caused by aphids to plants. The number of aphids that cause damage by sucking the plant juices is generally much higher than the number of aphid vectors that cause damage by transmission of a disease. This different threshold is thus important with respect to parasite effectiveness as well. We know today that the parasitization of an aphid in a plant cannot prevent the transmission of a virus disease. On the other hand, the parasites may cause a decrease in aphid vectors in limiting their number prior to their emigration to other habitats; however, total eradication of an aphid vector population by parasites in a given stand is relatively rare in nature, and the small number that escapes is sufficient to cause damage to other plants. We can see again how the significance of parasite action can be different.

The meaning of effectiveness has been commonly used for the feature of a parasite species to limit or control the aphid host to a different degree. However, for example, people searching for parasite species in the initial phases of a parasite introduction program report some species to be effective. Similarly, many field observations, undertaken in short periods during the season, may show a high or low percentage of parasitization (number of aphid mummies observed in the colonies) and correspondingly, the parasite is referred to as effective or ineffective. Therefore, on the one hand, the meaning of effectiveness of a parasite is used as the character of a certain period of its seasonal history with respect to a given host species, on the other hand, it is used as general information or brief characteristic of a species based on short-time observation. There is no doubt that in both cases the same expression is used, although the true meaning is not identical, depending on the point of view. We know that effectiveness of a parasite in nature is no constant or even a specific feature: potential rate of increase is surely specific, but it depends on the environmental forces whether the parasite may realize this rate (see above, definition of effectiveness). Strictly speaking we should not theoretically classify certain species as effective ones, but as being effective under certain given conditions. Nevertheless, in praxis it is different. There are quite a number of cases when no comparative classification or detailed data on the conditions under which the parasite is effective are available, effectiveness is commonly mixed with percentage of parasitization, etc. But, on the other hand, we are glad, in many cases, to have at least such field records on the separate species or those giving at least a brief note. Thus, we ourselves often use the classification of a parasite species to be more or less effective in a rather general way, although having in mind the complex and complicated matter connected with the effectiveness of parasites.

In the laboratory, we simplify the complex action of factors influencing the parasite effectiveness in nature in that we deal with the influence of the separate factors in a separate way. Thus, when the action of many environmental forces is restricted in this way, the parasite exhibits different effectiveness than under the

complex influence of a natural environment. This phenomenon must be always kept in mind. In the laboratory, we can recognize very well the potential rate of parasite increase as well as the influence of isolated or partially complex action of various environmental factors; the elaboration of life-tables, although being rather useful, can help us to understand the influence of only some of the environmental factors whose action in nature is rather complicated through their complexity.

A high percentage of parasitization seems to influence us in classifying such a species of parasite to be an effective one. However, as may be seen from the review of factors that influence the parasite effectiveness, this may or may not be so. A parasite can be effective when parasitizing a really high number of host individuals, but, on the other hand, the significance of a parasite may be higher if it attacks a relatively lower number of host individuals but in a period of low host density: thus, the percentage of parasitization may be low, but the parasite is more effective. Therefore, we must emphasize that effectiveness of a parasite species and percentage of parasitization are two different things.

— **FACTORS.** In parasite effectiveness, as mentioned in the definition, both the intrinsic phenomenon of the parasite and the environment are important. Correspondingly, we have listed the main factors, which could be divided into three groups, i.e. intrinsic features of a parasite and influence of the abiotic and biotic environment on the parasite. It is obvious that the action of these factors is complex and the relations among them are rather complicated. We have dealt with the separate factors in various chapters of this book in a more detailed way, so that they are only briefly listed below:

1. Fecundity.
2. Longevity.
3. Rate of development.
4. Oviposition.
5. Mating.
6. Self-regulation mechanism of parasite population (intraspecific competition, dispersal, decrease of daily reproductive rate, sex ratio).
7. Host specificity (searching ability, host instar preference, host range, host suitability).
8. Adaptation to the life-history of the host.
9. Host density.
10. Host plant.
11. Temperature and relative humidity.
12. Photoperiod.
13. Distribution.
14. Character of stand.
15. Period of the season.
16. Action of other natural enemies.
17. Hyperparasites.
18. Man's activity.

— **VARIATION.** As parasite effectiveness is a result of interaction between the parasite and the environment it does not have a constant value, but changes as to time and space.

Intrinsic features of separate populations may differ so that the parasite populations may exhibit differences in time and space. We know cases where early spring population and summer populations occurring at the very same locality differ from each other. Further, populations occurring in different parts of the distribution area differ from each other as well.

Similarly, the conditions of the environment change at the same locality during the season, a year or different years. Further, the conditions of the environment differ in space as well—there are different conditions in separate climatic zones, habitats, and microhabitats.

Control

Damage caused by aphids to plants represents different kinds: the aphids cause weakening and deformations of the attacked plants; they produce honeydew which can serve as a medium for the development of fungi, and finally, the aphids act as vectors of virus diseases of plants.

Plant weakening and deformation of attacked plants is a relatively long process which needs a certain interval before damage is caused. However, because of the balance of nature, the parasites act mostly at such a period when the aphids like caused damage and reduce their numbers. Significant action of parasites at the initial period of aphid population development is relatively rare. Thus we must classify this feature with respect to aphid control in such a way that parasite action cannot prevent such damage caused to plants by aphids as leaf curling, galls, etc.: the aphids may be considerably limited by the parasites only after the plant deformation had developed. This feature needs corresponding activities in integrated control in the timing of treatment and use of selective insecticide. There could be another situation if an aphid causes weakening of plants but it does not reach economic injury level, or does so only in a certain part of the season; in such case, which seems to be quite common among the aphidiids, parasite action is useful and may be supported by proper use of a selective insecticide to prevent an aphid outbreak and so decrease aphid population equilibrium level in a certain part of the season.

Honeydew production, when it may be significant to cause trouble in harvesting of crop (alfalfa) or serving as a medium for fungi, is a by-product of a high aphid population level. The control activities are principally the same as in cases mentioned earlier.

Virus transmission by aphids and their limitation by parasites is a different case. The number of aphids - vectors may be considerably reduced by the parasites, but the remaining aphids are sufficient to cause damage to other plants by virus transmission (alate aphids namely). Thus parasites can cause a certain reduction of aphid population either on another plant or on a given crop, they can also limit the number of actual or potential vectors, but they are not able to prevent virus transmission. Even if the aphid vector is parasitized, the disease is transmitted, as the interval of transmission is much shorter than the period during which the parasite kills the aphid. This feature of parasite effectiveness must be kept in mind when an integrated control program is elaborated. Probably the parasites might be useful in reducing the number of aphid vectors in their sources (weeds, etc.), but they are not able to prevent an aphid vector attack on a crop.

- **VALUE OF PARASITES.** The principle must be kept in mind when evaluating the aphidiids for aphid control purpose, that the parasites are only a part of the whole natural enemy complex and they may have a different position and role regarding time and space: they may be effective only in certain parts of the season, they may occur in some microhabitats only, they exhibit a certain mode of dispersal, etc. In such a way, the parasites differ from other members of the natural enemy complex, however, we must stress the fact that natural enemy action is complementary. In an aphid control program, we must evaluate the role of separate natural enemy groups during the season and select the most suitable period for eventual treatment, etc.

- **APHID POPULATION EQUILIBRIUM.** Equilibrium position of pest aphid population in a given community, the fluctuations around this position, and the significance of natural enemies (including parasites) must be capable of limiting the aphid population fluctuation below an economic threshold to a various degree in different parts of the season or years.

- **STAND AND SEASONAL HISTORY.** The kind of stand where the aphid pest occurs and has to be controlled is rather important for an aphid control program. It is generally known that in mixed stands the aphids are better limited by natural enemies than in pure stands. Crops grown by man represent mostly pure stands. Further, it is important whether the crop is annual or perennial as more stable communities occur in perennial crops. The aphid life cycle is also important as the aphids are capable of

emigrating or immigrating to a stand during the season, the effect of aphid emigration or immigration being different depending on the character of the stand. However, with respect to the control, single environmental factors that predominate can often be demonstrated in more simple communities, as correctly stated by DEBACH (1958).

— VARIATION OF APHID FAUNA. In a given area, a certain aphid fauna is associated with a certain crop (plant) as a part of the agrocenose (natural community). The qualitative composition is practically constant, but the relative significance of the separate species changes according to the season, year, etc. The same is true as to the parasites.

In a broader sense, in a wider geographical area, the qualitative composition of aphids and parasites changes considerably, as it is influenced by various climatical, historical and other factors. Similarly, the significance changes too.

— ORIGIN OF THE PEST. The knowledge of the origin of pest aphid species may be helpful in understanding some features of the natural limitation of the aphid pest by parasites in a given community. Indigenous parasites may adapt to a new immigrant in a various degree: for example, there has been almost no adaptation of native parasites to such pests as *Therioaphis trifolii* or *Chromaphis juglandicola*, which were introduced into California. On the other hand, we know a number of aphids which were distributed and became established also in indigenous communities in a new area and are attacked by indigenous parasites as well, the latter exhibiting various degree of significance. *Toxoptera aurantii*, a pantropical and pansubtropical pest, which has become distributed due to Citrus growing, is a good example. The occurrence of various faunistic complexes and host range of their members in a given area seems to play the main role in such cases.

— MAN'S INFLUENCE. It is well known that man has influenced the environment to a great extent. The changes of the environment have naturally influenced the limitation of aphids by parasites. We can recognize quite a series of such cases. Truly natural communities, such as those preserved in National parks, or virgin lands, exhibit the original state. Then, there are quite a number of semi-modified environments where the environment has been influenced but not basically changed by man, and as, apparently an extreme case, there have developed communities due to man's activities, the agrocenoses, which developed on man's activity as to their occurrence, being strongly influenced by the neighbouring communities. The development of such communities which are partially artificial when compared with the natural communities, have been also associated with the development of special relations among their members: it is generally known, that the number of species in such communities is lower, and the population level higher, when compared with the state which may be found in the neighbouring more or less natural stands.

Natural limitation of aphids by parasites (natural enemies) in agrocenoses, which has developed due to equilibrium position in such communities, is influenced due to harvesting practices, irrigation, ploughing, etc., or even by chemical treatment by an insecticide which is applied to control another pest. Intentional changes to decrease the aphid population occur in case that the aphid has become a pest: man tries to protect the crop in developing aphid control measures (chemical, biological), and then integrated control programs have been developed to control pest aphid populations present on crops. In an integrated control program, natural limitation of aphids by natural enemies (parasites) is the base of the program, being completed by control activities.

— PARASITE INTRODUCTION. Introduction of parasite species from abroad is one of the means of aphid control. Natural conditions have to guide us both in selection and

the number of species introduced. As the limitation of aphids by parasites (natural enemies) is made by a number of species, a similar state must be developed in the control area. A greater number of established parasites (natural enemies) contributes to the stability of the environment. As it is obvious from the development of populations of introduced pest species, every community tries to limit the population increase of a new immigrant; however, it succeeds to a various degree, the latter being especially true for the agrocenoses, thus, we may help such a community in artificially adding the agents that are temporarily lacking in the community, and in this way help to develop at least a partial "natural" limitation through control activities.

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Biological Control of Aphids

PRINCIPLES, TERMINOLOGY AND TRENDS. Biological control means a direct or indirect manipulation by man of living natural organisms on pest organisms, in deliberate attempts to reduce populations of the latter to such levels that economic damage is eliminated or significantly reduced (see: BEIRNE 1962).

In this respect, we follow FRANZ's (1962) terminology, separating the natural state which occurs in the environments without man's purposeful action, i.e. natural limitation (or regulation), from the purposeful manipulation of organisms in an environment by man, i.e. biological control.

Biological control of insect pests by biotic agents is known to have a long history, during which various trends have developed and been followed. From another point of view, we recognize the empirical and scientific approach to the problem. This approach, however, although recognizable in dependence on the history too, has been known to depend on the state of other branches of entomology, namely of a basic research trend, which may cause the biological control work to start on an empirical basis although the true biological control work should be really scientific. This state is due to unequal and unsynchronized development of the basic and applied research. Even at the present day we also can find a case, when a pest is introduced into a country and a search for natural enemies in its native country is then undertaken to translocate the enemies into the country of pest introduction. Although this activity may be based on a well based scientific program, we can recognize when searching for the enemies, that there are no records on the parasites known, or only poor ones: the taxonomical value of the species is unknown, not to mention the biological data; thus, we have to introduce a complex of natural enemies on which we have no basic data—although today's praxis is based on postintroduction studies, there is no doubt that general distribution, habitat distribution, host range, etc. in separate parasites should be known. This state, naturally, can make the biological control praxis rather empirical at the initial stages of research, although its further development is really scientific. We could perhaps mention here a well known case of biological control, the control of *Therioaphis trifolii* in California, and the development of our knowledge of its parasites, starting from their identification.

Three main approaches are usually distinguished in biological control: (1) Permanent control, (2) temporary control, (2) intensification of existing control (BEIRNE, 1962).

The aim of permanent control is to develop purposefully a perpetual control of the pest in a given country. This is the most common trend in biological control. The purpose of this trend is obvious: if there is a pest, either indigenous or introduced, in a given country, man tries to use biotic agents to keep it under control, and, naturally, such an activity is the best if it results in a more or less perpetual state

useful for man. Aphid parasites have also been mostly used for such a purpose. Aphids, both indigenous or introduced species, cannot be eliminated in a given country as a part of their distribution area, but their numbers are known often to be considerably reduced because of the action of natural enemies in nature, and relation of the aphids and their limiting agents is used by man purposefully.

Temporary control means the application of biotic agents with the aim of obtaining a temporary result, which is usually required to be rapid in action; perhaps, the biotic agents could be classified as "biotic insecticides" in this respect. The aphid parasites, just because of their manner of action, do not seem to be useful for such a purpose; even the mass-utilization of adult parasites does not mean that the pest will be rapidly controlled as, (1) the parasite development lasts several days before the aphid is killed, (2) the parasite population tends to disperse to prevent overpopulation, and (3) even the ecosystem tries to suppress such an artificially developed parasite overpopulation state. Moreover, an immense number of parasites would be necessary for such a purpose, and this would require a relatively costly process connected with mass-rearing, etc. (see: CLAUSEN, 1958).

Intensification of biological control. The third approach means the modification of the environment to favour existing natural enemies, whether indigenous or introduced, at the same time, without favouring the pest (BEIRNE, 1952). The application of this trend, aiming principally at the conservation of parasites, seems to be rather perspective in aphid parasites.

There is a principal criterion in biological control as what degree of control can be classified as a success. BEIRNE (1962) uses four degrees to evaluate success in biological control: (1) perfect success, when the control of the pest is so efficient that it reduces the pest population to a level at which the agent can no longer find sufficient specimens to attack, and consequently it dies out, thereby enabling the pest population to increase; (2) fully successful attempts, where commercial damage is eliminated; (3) partially successful attempts if the level of the pest is significantly lowered; (4) nominally successful attempts if the agent is established but does not increase significantly.

As it is generally known, the nature of a given ecosystem in which a pest aphid has to be controlled, influences the degree of success considerably. For example, we can expect biological control to be successful in stable environments, while in unstable environments, such as annual crops, the parasites (natural enemies) will hardly be capable of keeping a pest aphid under successful control. Consequently, integration of control measures is necessary.

APHIDS AS CONTROL OBJECTS. STERN *et al.* (1959) characterized very briefly and usefully the increase to pest status of a particular species.

1. By changing or manipulation of the environment, man has created conditions which permit certain species to increase their population densities.

Aphids are a spectacular example of such pests. Monocultures of crops are known to create rather favourable environments for the enormous increase of aphid numbers all over the world, from the temperate zone to the tropics. Besides the monoculture character of the stand, even such manipulation of the environment by man, such as treatments, may be rather favourable for the rapid development of the remnants of a treated population as well as for the immigrant populations to reach economic level numbers rather quickly due to the adverse influence of the treatment on aphid natural enemies. Besides these phenomena, which are more or less man-dependent, the aphids are rather dangerous pests because of their migration, either obligatory or facultative, as they can either occur perennially in a crop environment (and

disperse from there by migration), or they seasonally immigrate and emigrate to a crop environment; the last feature is rather difficult with respect to aphid control as the sources of the pests are mostly outside the crop environment, often uncultivated or natural stands. Thus, because of the monocultur character of the stand, certain features of application of chemicals by man to control the pests and a number of features in their biology, aphids can be considered serious economic pests.

2. Through transportation across geographical barriers while leaving their specific predators, parasites and diseases behind.

We know quite a series of cosmopolitan aphid species which are simultaneously known as cosmopolitan pests, either polyphagous or being associated with certain crops. It is known that aphids are often transferred during transportation of vegetables, seedlings, etc., to the whole world: their passive dispersal over great distances is also known. Although being sometimes seasonal, their parthenogenetic type of reproduction allows them to become established in new favourable environments very quickly, also in a very sparse initial population.

Today, we are able to recognize the history of distribution of several such cosmopolitan pest aphids. For instance, as the history of Citrus growing over the world is relatively well known, we can ascertain the probable date of establishment of *Toxoptera aurantii* in various parts of its present world-wide distribution area, which covers the subtropical and tropical belts, where it was introduced with Citrus introductions, while being southeast-asian in origin.

Even in quite recent periods, we have had the possibility to observe the accidental introduction and further development of aphid populations in new environments, where they reached outbreak numbers rapidly and became serious pests. *Therioaphis trifolii*, an inhabitant of the Old World, which was accidentally introduced in 1954 into California and became a serious economic problem, may be mentioned.

3. Establishment of progressively lower economic threshold.

This criterion is responsible for keeping the aphids as economic pests in many cases in which they were earlier classified as pests of subeconomic significance.

Aphids are known to occur in the greater part of the environments on the earth. For this reason, there is a great number of natural enemies and diseases which attack them.

Thus, if we summarize our knowledge with respect to biological control, it is obvious that, on the one hand, the aphids are serious pests of economic crops, on the other hand, there is a great number of various natural enemies known over the world. Consequently, there is a great possibility to use certain of these biotic agents that can influence the aphid numbers in the purposeful control of aphids. There is no doubt that the peculiarities in aphid biology cause many difficulties in their biological control which would appear to be discouraging, on the other hand, we are at the very beginning of this complex research and the successful results reached in control of some pests, such as *Therioaphis trifolii* or *Acyrtosiphon pisum* are encouraging.

INJURY CAUSED BY APHIDS. Aphids rarely cause serious damage to healthy plant specimens, attacking and causing injury mostly to less developed individuals. They naturally may be found to occur on healthy individuals as well, but they do not cause there any apparent injury because of the quality of the plants, and on the other hand, in natural communities really heavy outbreaks of aphids are relatively rare. From the community point of view, in a similar way as other phytophagous insects, aphids may be considered to be partially useful in taking the part in natural selection of a part of plant population in natural communities—plants which are attacked may become less successful in interspecific and intraspecific competition.

As shown above, community balance keeps their population fluctuating around a certain equilibrium.

On the contrary, in cultivated environments, owing to a number of reasons such as the character of monoculture, stability of stands, etc., aphids often find an occasion to reach outbreak numbers and cause heavy injury to crops grown by man.

— **KINDS OF DAMAGE.** There are several kinds of damage in which an aphid may cause injury to the attacked plant. We have summarized the injury caused by various aphids into several categories, but several kinds of injury can occur simultaneously.

1. Sucking of aphids affects the attacked plant in two ways: on the one hand, there is a general weakening of the plant. This may be observed as a general weakening, inability to reach maturity, reduction of vitality, discarding of blossom and fruit, reduction of size and quality of fruit, worse photosynthesis, poor ripening of wood (may easily become frozen). On the other hand, aphid sucking stimulates the plant tissues in a peculiar way, which results in a change of colour, dwarfing of stems and leaves and development of galls.

2. Honey-dew, when produced in greater quantities, covers the leaves and causes difficulties in respiration and assimilation. Moreover, it represents a favourable medium for various saprophytic moulds. On the other hand, honey-dew represents a source of food for adults of many beneficial insects that attack the phytophagous organisms which infest the given plant or other plants in a given community.

3. Aphids are known to be capable of transmitting a great number of viruses of plant diseases.

— **CRITERIA.** Injury caused to crops by aphids can be classified from three viewpoints:

1. Season and length of occurrence period. It is important for how long and in what part of the season the injury has been caused by the aphids. Even the same kind of injury caused by different pests may be different because of different lengths and periods of the season. For instance, in C. Europe, as mentioned by WILDBOLZ (1966), the most abundant of all migrating apple aphids is *Rhopalosiphum insertum*. As this species leaves the apple tree for the summer host already after blooming, and it does no damage to the fruit, its economic importance is slight. Far more dangerous is *Dysaphis plantaginea* which occurs only in small numbers in spring, but which stays until mid-summer on the apple tree, increasing to considerable numbers under favourable conditions and causing fruit damage.

2. Relation of the injury to plant. Injury caused by aphids may be restricted to one season, or the results may occur for the whole life of the infested plant. Age of the plant and kind of injury play a role. Virus disease transmission affects the plant for the remainder of its life, both in annual and perennial crops. Leaf-curling, fall of blossoms, honey-dew cover on leaves, all this is restricted to one season and only partially influences the overwintering or plant quality in the next season; however, this is true for the older trees, while deformation of seedlings due to aphid infestation may have an adverse effect on the infested plant for the rest of its life. For example, *Aphis pomi* occurs perennially on apple trees, causing leaf-curling. However, while its significance is lower in older trees where it is restricted to young shoots, its infestation of the nursery trees often results in heavy deformation of the whole top of the infested plant. Similarly, *Aphis spiraeicola* causes heavy deformation in younger or nursery trees of Citrus, while its occurrence on older trees is less dangerous.

3. Relation of the injury to harvest. The point of view of the harvest, the quality of the harvested part of the crop as well as of harvesting practices is usually taken first into consideration as it is practically an immediate result of aphid caused injury. Besides weakening of plants, difficulties may be caused during the harvest due to accumulation of honey-dew covered plants (alfalfa). Similarly, besides the decrease

of production of the trees in orchards due to a worse assimilation, fall of blossom and fruit, etc., the fruit can be deformed due to aphid sucking or covered by mouldy honeydew and not suitable for the market. Such cases are rather numerous.

LABORATORY. The equipment and organization of insectariums have been widely mentioned, described and discussed by FISHER & FINNEY, (1964). Generally, each insectarium is deeply influenced by the objects which are dealt with, only some general rules and facilities, widely reported by the quoted authors, have similar features. The insectarium facilities and equipment are naturally influenced by financial costs. It is not our intention to deal here with the general classification of insectariums. We decided, mainly as a result of our own experience, and to a lesser degree as a summary of visits of some insectariums abroad, to present here a scheme of insectary work with aphid parasites for the purpose of a biological control program. Mass-rearing procedures, etc., are dealt with in a separate part in further detail.

A temperate climate zone seems to be the most suitable for the location of a biological laboratory (insectary) complex. A temperate environment is better than subtropical and tropical areas, where climatic influences need expensive facilities for cooling, this latter being necessary only during a part of the summer months in a temperate area.

The best situation for a biological control laboratory is generally said to be away from the immediate vicinity of cultivated (agriculture) areas because of possible influencing of insecticidal treatments used in the fields, in addition to preventing accidental inter-contamination of the cultivated areas by pests and parasites. On the contrary, the location of an insectary in a place where urban or industrial atmospheric contamination is a problem, should be avoided too (FISHER & FINNEY, 1964).

Therefore, in a temperate zone, a biological control laboratory area should be located in smaller towns or villages, at a certain distance from large towns, where, nevertheless, there are good transport facilities.

As is obvious from the following, we classify a biological control laboratory as a complex of units, which should be assembled together at one place.

- *Office laboratory.* This is the very room where research workers do their work. In this laboratory, microscope, photography and other technical equipment is deposited. Card indexes include records on host and parasite as well as records on their introduction, laboratory stocks, etc. A small library containing the basic textbooks on biological control, host and parasite biologies, is recommended, being completed by a comprehensive collection of papers on individual problems. In this laboratory, too, a collection of mounted parasites is deposited, partly because of the work of the scientist on the group as a whole, partly due to deposition of mounted representatives of various laboratory stocks for further reference. As to furniture, several laboratory tables, chairs and cupboards are necessary in order to distribute all the above mentioned equipment in a useful order.

- *Quarantine laboratory.* A quarantine laboratory, with respect to aphids and their parasites, is usually best situated as a part of the biological control laboratory. Its basic function, as defined by FISHER (1964), is to provide facilities which will permit the handling of imported material in a manner that precludes the escape of potentially dangerous organisms.

Minimally, a quarantine laboratory should consist of two separate rooms: the first room is an anteroom, where a source of light is situated as a trap for possible insect escapes. Special coats should be worn by the workers and used in this laboratory exclusively, decontamination being necessary in case that research workers leave the

laboratory. In this room, the quarantine activity begins. A double-spaced window (with lights fixed in the inside window), or a strong electric light with a pane of glass placed in front, represent the source of a one-sided light. Otherwise the equipment is the same as in the biological control laboratory unit, except that the quantity of tubes, cages, etc., necessary for the propagation is more numerous; the latter, too, not being used except in contact with the introduced material. According to FISHER (1964) minimum plumbing facilities should include a sink equipped with hot and cold water. Desirable additional facilities are distilled water, gas, air vacuum, air pressure, and carbondioxide gas in both the anteroom and quarantine room. If possible, a toilet and washroom containing light traps should be provided for the use of the quarantine personnel only. A small autoclave is recommended in the quarantine laboratory for sterilization of received material. After the received shipment is selected, all unnecessary material such as cartons, boxes, etc., should be placed in a large plastic bag, carefully closed and later burned.

— *Laboratory rearing rooms.* It is a principle to have for each host and parasite a separate rearing room. This prevents an accidental inoculation of host rearings by parasites, of mixed colonies of hosts, etc. However, even here we have various light traps to catch accidental escapees. Such rooms must have automatically controlled temperature, relative humidity and light conditions. Air circulation is necessary. It is recommended to change temperature and humidity conditions between certain limits, which are regulated according to host and parasite temperature requirements.

— *Controlled temperature room.* In this room, all the equipment for the rearing of material under strictly controlled conditions is placed together. Thus, we put there a series of incubators, in each of which we have a certain temperature environment. Refrigerators are also placed in here: one refrigerator, a large one, has to preserve relatively higher temperatures ($+10 - +14^{\circ}\text{C}$) for the storage of reared material, another one serves for experiments with a low temperature influence on parasite survival, etc. Because of cooling possibilities, it is advantageous to acquire such a room in a cellar or at least on the first floor, a northern position being the most suitable because of relatively less trouble due to high temperatures during the summer months.

— *Technical equipment room.* Biological control work requires a number of different facilities. Many of them are not needed immediately, but must be at hand when necessary otherwise it could take a certain time to acquire them and possible unwanted changes in the program would follow as a result when they are obtained and carried from out of doors. It is important to have such equipment and it must be deposited somewhere. A technical equipment room is such a place. Rearing cages, nylon textures, various containers for parasite transport, release, plant rearings, etc., all represent the equipment which is deposited in the technical room.

Other necessities, such as washroom, closet, etc., are not mentioned here.

— *Specialized research equipment.* Specialized research equipment of proved value for determining biological potentials is the bioclimatic cabinet, where various factors (light, rel. humidity, temperature) can be automatically controlled (for a detailed description see: FISHER & FINNEY, 1964).

— *Heated greenhouse.* During certain periods of the season a heated greenhouse represents a rather useful place, although it can be in function perennially as well. The heating in a greenhouse makes it a rather valuable environment during the winter months, including the late autumn and early spring; during this period, we have no possibility of growing the aphid host plants in the open because of frost and snow. Further there is no danger of accidental introduction of various out of doors insects to the greenhouse, which together with high summer temperatures, decreases the

value of a greenhouse during the summer months. In the winter months, a heated greenhouse can be useful, not only for the growing of plants necessary in laboratory rooms, but in the direct rearing of host aphids and parasites. This is advantageous when masses of material have to be produced.

A heated greenhouse, the same as laboratory rooms, is recommended to be divided into several boxes at least which permit the separation of material such as culture of host plants, host aphids and parasites. However, it is obvious that greenhouse conditions—due to conditions of temperature—must be only general as we shall have no possibility of controlling the conditions in the separate boxes. Thus, different species reared will find the same environments to be suitable to a various degree: *Acyrtosiphon pisum*, for example, prefers lower temperatures, while *Aphis craccivora* reproduces better under higher temperatures. Even if we have an anteroom in a greenhouse and all the boxes are well separated, greenhouse conditions enable accidental introductions of the reared material to a higher degree; therefore it is recommendable to select the material which is planned to be reared in a greenhouse, to prevent the development such mixed cultures. For example, we have found it almost impossible to rear *Acyrtosiphon pisum* and *Aphis craccivora* in the same greenhouse, as they were both reared on the same species of Leguminous plants and *A. craccivora* dispersed readily to other boxes. Mixed colonies of aphids were rather unfavourable, as both the species were differently successful in competition depending on temperature; although their parasites were specialized, the changes in host populations were highly undesirable. On the contrary, the rearing of aphids such as *Hyalopterus pruni* on the common reed, *Phragmites communis*, and *Acyrtosiphon pisum* on alfalfa, and their associated parasites, did not bring about such trouble.

In a heated greenhouse, besides the controlled temperature within certain limits, the control of light period, light intensity, watering and air circulation is necessary.

FINNEY & FISHER (1964) classified greenhouse facilities to be necessary for the culturing of the host plants, but, in general, it is believed that a greenhouse does not provide an ideal environment for the mass-culture of entomophagous insects because of factors which are largely beyond the control of the insectary operator: light and relative humidity conditions cannot be economically standardized; contaminant species of phytophagous insects will invade the plants, and predators and secondary parasites cannot be excluded. We fully agree with these statements, although we believe that most of them can be excluded during the late autumn-early spring period and thus make greenhouses useful environments during certain parts of the season.

— *Non-heated greenhouses.* A non-heated greenhouse can be advantageous in early spring and the spring period for the growing of plants, and even for host and parasite mass-production. Accidental introduction of secondary parasite and aphid predators is common, but when the reared material is planned to be released during spring, the undesirable natural enemies usually do not reproduce too much.

Later in the season, when temperature conditions become too high and unfavourable, we remove the glass from a part of the windows and replace it with nylon texture. Then if air circulation is controlled, such an adapted greenhouse can serve as a large semifield rearing cage.

— *Experimental plots.* A smaller plot in the open must be selected in the neighbourhood of the biological control laboratory. Here we grow the host plants and make experiments with the host and parasite material under semi-field conditions. In this plot, too, we can construct large nylon cages and rear the host and parasite populations in the open and observe the development of the populations during the whole year. Winter survival of introduced parasites and the coincidence of host and parasite appearance can easily be observed just in such conditions.

Program

ECOSYSTEM. The research of the ecosystem to which a given aphid pest belongs is of basic importance for biological control work. The relations which occur in the given environment enable the given aphid species to reach certain levels and become a pest. To recognize such relations enables us to manipulate the given environment purposefully, with the aim of keeping the pest aphid population number below certain levels which are determined by the degree of injury it causes to certain plants.

Biological control work deals with the biotic agents of ecosystems, which, naturally, cannot be separated from the whole complex of the ecosystem. The environment is known to influence the role of natural enemies (parasites) to a high degree.

Most biological control objects, the pest aphids, occur in agro-ecosystems, which are associated with cultivated crops. Agroecosystems are known to have peculiar features in which they differ from the natural stands. Stability of the system in which biological control has to be applied is one of the basic research problems. Similarly, as in other research trends, a given ecosystem in which biological control should be applied, cannot be separated from the neighbouring ecosystems because of many interrelations.

HOST PLANT. Two viewpoints are used when we classify the host plants. First, field information is necessary suggesting whether the plant is an annual or perennial crop, whether it represents sufficient shelter for parasites, further, the growth phases of the plant and coincidence of the pest as well as the influence of the pest on the plant. Second, the host plant is evaluated for eventual growing under laboratory conditions, whether it is available and useful as a host plant for rearing the pest in the laboratory, what kind of substrate it requires, etc.

PEST APHID. 1. Taxonomical classification of the aphid is important. Some species are taxonomically rather different from the indigenous fauna, others may be closely related. There may be even taxonomical vicariants. Phylogenetic age of the group to which the given species belongs is also important. It is well known that phylogenetically older species often exhibit a more specialized parasite fauna than the younger species: for example, if there is a callaphidid pest aphid, it is obvious that its parasites will be mostly strictly specialized, while in case of an aphidine pest the parasite fauna may be widely specialized.

2. It is necessary to know the origin and history of distribution of the pest species. This helps, on the one hand, to understand its pest status, on the other hand, this is necessary for the search of natural enemies over the world. On the basis of such information we are able to predict how an introduced pest will probably behave in a new environment, as similar cases may be known from other parts of its distribution area. The data on the origin and distribution of the pest further enable us to classify whether the pest is indigenous or an introduced species with respect to the given country. Furthermore, in a newly introduced pest, the records on its occurrence and host range over the world enable us to predict what host selection and occurrence in habitats will probably develop in the newly introduced pest, as climatic conditions through the occurrence of various communities influence an aphid pest considerably. For example, *Toxoptera aurantii* which is today a cosmopolitan subtropical and tropical pest, has its home in southeast Asia, where it attacks a rather wide range of host plants. It also does so in other parts of the tropical belt, in which it was accidentally introduced (Cuba, etc.). However, in the subtropics, such as in the subtropical

U.S.A., or in the Mediterranean area (S. Italy, Israel, Black Sea coast, etc.) or in S. America, its host range is restricted so that perhaps it attacks only Citrus, Thea and Camellia; all these plants are either crops or ornamentals and this restricts also their occurrence to various habitats to a considerably degree. Thus, it is obvious that the control of this pest in the subtropics could be much easier as it is restricted to several plants and habitats, while in the tropics it becomes a common member of various (forest-type) tropical communities and its control would be much more difficult, as the sources of the pest remain continuously in a number of habitats. Similarly, as another example, it was expected soon after the introduction of *Therioaphis trifolii* into California that it would spread rather rapidly and in a wide area, and it did so, because of favourable environmental conditions (climate, host plant, irrigated lands, etc.).

The origin of the pest is also rather important for the evaluation of the possibilities of its control in a new country. As mentioned by BARTLETT & V. D. BOSCH (1964), pest-immigrants are for the time being the more common projects for success than are the indigenous pest species; although some native species have been controlled by purposefully introduced natural enemies in past campaigns, the number of such cases is low when compared with the control of immigrants; this is true for the obvious reason that native pests are usually already attacked by a complex of natural enemies which have evolved with them. Although this aspect is generally true, we should, however, take into consideration that the character of the stand (agroecosystem) may be helpful because of the existence of gaps in the limitation of the native pest by native enemies, and an introduced natural enemy could cover these gaps. Nevertheless, it is also true that very few attempts or even successes of this kind are known. Furthermore, a pest may be primarily an introduced species, but its introduction may be of an old date so that it has become a common member of many indigenous environments, and indigenous natural enemies have adapted to attack it; *Toxoptera aurantii* in various parts of its distribution area could be mentioned as an example, moreover, the adaptation of indigenous natural enemies to a new pest is also rather important for selection and introduction of parasite species.

3. Field information on a pest aphid in a given country, which must be connected at least with general literary information, must include the life-history of the aphid, its seasonal occurrence, the habitats in which it occurs and the host plants attacked. This knowledge enables the classification of sources in which the aphid occurs during the season and from which it spreads to other areas; the relation of wild or semi-cultivated environments to the cultivated areas is rather important from this respect.

4. Laboratory information on the species must be obtained with respect to the pest and with respect to its rearing. The information on the pest aphid must include at least the main biological data on the rate of development, fecundity, etc., while information on rearing conditions, such as regulation or parthenogenetic cycle, laboratory host plants, requirements on physical environment, etc., are important for successful continuous rearing.

5. The principle kinds of injury caused by the pest to the crops must be known as they can influence the methods of control considerably. It is necessary to know in what part of the season, in which habitats it occurs, and what kind of injury is caused to the crops. The significance of parasites as possible control agents is known to be different: they mostly come into action after, for example, leaf-curling and galls have developed, while their role may be different with respect to plant weakening by aphids, similarly as it is different in case that the pest causes injury mainly as a vector of plant virus diseases.

6. Control problems. The classification of the ecosystem and of the pest allow us

to acquire general information about the position of the pest in a given country and general problems arising with regard to its control. This is rather helpful for further work on natural enemies as well as in an integrated control trend.

INDIGENOUS PARASITES. 1. Specific composition of the parasites that attack either an indigenous or introduced pest in a given country may be relatively easily recognized by collecting and rearing of aphid colonies, the samples being taken throughout the season in all the different habitats in which the pest occurs. Qualitative analysis of this type is known to be a relatively long-termed question when having to be detailed, while a general idea about the parasites may be obtained in a relatively short period if the research is undertaken methodically. It is obvious that good taxonomic elaboration, where such information is obtainable, is rather useful for biological control purposes.

2. After the specific composition of parasites is known, their general distribution must be recognized. Knowledge of the whole distribution area and occurrence in various habitats is useful for classification of the relation of the pest and indigenous parasites and eventual further search for better adapted races and strains for intraareal introduction.

3. Field information on separate species. It takes a considerable amount of time to acquire detailed field information on the separate species: the best may be obtained by complex research of the group, when all the aphids and all the parasites are collected in different habitats and in different seasons of the year. We can, however, obtain better information on separate species only with difficulties when starting research with the parasite species and endeavour to find their hosts in various environments. Complex faunistic elaboration of separate countries or areas is rather useful; in case of their lack, at least records from neighbouring countries can be used for general information. Field information on the indigenous species should include the occurrence in separate habitats, host range, foci in nature, seasonal occurrence and field records on the effectiveness of the parasite (at least general observation on the occurrence of mummified aphids, etc.). Because of the knowledge of the pest origin and distribution area of the parasite we can derive whether the parasites are truly indigenous with respect to the pest or whether they have adapted only secondarily to the pest; the latter is important just in pests that have been introduced in earlier times and have seemingly become native inhabitants of various environments in a given country.

4. In the laboratory, we rear the separate species that were preliminarily found to be significant in natural limitation of the pest in a given kind of habitat, the main aim being to recognize their requirements on the physical environment, host and parasite relations, and laboratory effectiveness.

5. The comparison of both field and laboratory information enables us to evaluate, at least in general features, the role of indigenous parasites in the limitation of the pest in various habitats during different parts of the season. In case that general records on the action of other natural enemies are obtainable, this may show the reasons why the natural limitation is ineffective or poorly effective or why certain gaps in natural enemy action occur during the season. On this basis, biological control activities are undertaken.

6. Biological control

(a) Intraareal introduction. When the action of indigenous parasites is low, we try to recognize the nature of this phenomenon. Besides the environmental influences, this may have an intrinsic nature as the parasite may be found poorly adapted to the host or to a part of the climatic area. Thus, it could be advantageous to

introduce climatically better adapted strains from other parts of the distribution area U.S.A., or in the Mediterranean area (s. Italy, Israel, Black Sea coast, etc.) or in or such strains, which are better adapted to the pest. For instance, *Aphis spiraeicola*, which has become a pest because it spread to the southern areas of the U.S.A., the West Indies and the north of S. America, is attacked by an indigenous strain of *Lysiphlebus testaceipes* in California; this strain, however, is unable to complete its development when attacking the aphid, while a strain that occurs in the West Indies attacks the aphid successfully: it is obvious that intraareal introduction of the West Indian strain into California could be useful.

(b) Development of adapted strains, selective breeding. In case that there are no better adapted strains in the natural sources, there is a possibility of trying to obtain such strains first in the laboratory through selective breeding.

(c) Inoculative release. Inoculative release in the aphidiids was generally undertaken in the following two ways: on the one hand, material of parasites was transferred to the crop field and caged there in agreement with the confined release method, the cages were later removed and the parasites allowed to disperse and attack the aphid. This method, which was used, for example, by ARTHUR (1945) in control of aphids on cereals, means the inoculation of crop fields by parasites during early stages of pest occurrence, prior to their natural dispersal. Although good results (high degree of parasitization) were mentioned in the literature, the method seems to be restricted to experimental plots as the artificial dispersal and caging of the parasites is perhaps too laborious.

On the other hand, unmated aphids were mass-collected in the southern areas and transferred to the northern areas, where parasites emerged and occurred prior to their natural occurrence in the field. This method was used by HUNTER & GLENN (1909) in applying *Lysiphlebus testaceipes* in control of *Schizaphis graminum* and in *Lysaphidus platensis* (see MILLAN 1965). In general, this method tries to establish the parasites in aphid infested fields at an earlier period than they would disperse and occur in the fields under natural conditions.

(d) Periodic colonization. This means re-colonization of natural enemies following the adverse periods, so that a satisfactory balance between the host and natural enemy could be rapidly re-established (DEBACII 1964). This method does not seem to be practically applied in the aphidiids, although there are various projects of how to control the aphids by parasites in this way. In many cases, it is well known that the aphid and parasite population may become disjuncted during certain periods of the season (early spring, temperate zone) and it takes considerable time before the parasites are able to disperse from the focal points to limit them. Perhaps periodical colonization could be perspective in such cases.

(e) Changes in seasonal occurrence due to application of polyethylene plastic covers. We deal with this method in detail below as it was used primarily as a release method of imported parasites. Moreover, the results obtained allow us to consider that the application of polyethylene plastic covers could be advantageous: in early spring, the present populations of parasites (perennial crops) would develop and occur earlier in the field through the use of the covers and this might influence the development of aphid populations in the neighbourhood after these covers would be removed. Strip application of plastic polyethylene covers could be perhaps useful.

(f) Protection of foci, alternative hosts. Supplementary food is known to be important for a number of natural enemies of various insects. This has lead several authors to the research and experiments with growing various flowering plants (in forest protective belts, etc., MUSETSCHUKO 1949, etc.) to increase the concentration of natural enemies in such places and thus support their conservation and further

dispersal to cultivated surroundings. The aphidiids could be perhaps added (see: integrated control chapter) to such a program as alternative hosts of such species could occur in such stands being important for parasite conservation: generally, alternative hosts are known to damp oscillations in natural enemy and host densities, maintaining functional natural enemy populations during low density of preferred hosts, provide suitable overwintering hosts, facilitate maximum natural enemy distribution and reduce intraspecific competition (V. D. BOSCH & TELFORD 1964).

The role of alternative hosts is also important for the improvement of pest natural enemy synchronization. This is rather important in aphids, which are often known to be only seasonal pests, immigrating and again emigrating from certain stands in the course of the season. It is obvious that the presence of parasites in such habitats when they attack the alternative hosts, could be somewhat useful. FLANDERS (1949) suggested the planting of olcander in the proximity of citrus trees because of the conservation of alternative hosts of some parasites of citrus scales. We have proposed a similar manipulation of the environment with respect to the control of Citrus aphids in Italy (STARÝ 1964) as well as in Cuba (STARÝ 1968).

Indigenous parasite action is often influenced considerably by agricultural practices, treatments, etc. These influences are dealt with in the chapter on integrated control.

IMPORTATION OF FOREIGN PARASITES. At the first phase of parasite importation we summarize the data on the parasites of a given pest aphid species that were recognized to attack the pest in various parts of its distribution area. It is useful to elaborate general tables (see: distribution chapter) in which the list of parasites as well as the areas in which they are known to attack the given host are given. Further, as far as possible, the distribution of the parasites and their host range and, if any, further data on the biology are classified on the basis of literary records.

On the basis of the world species classification, which is more or less a theoretical question, we evaluate the distribution area of the pest and occurrence of parasites in various parts of this distribution area. At the present state of our knowledge the representation of parasites of various pests is rather incomplete, and the records are more numerous only in better known areas. Thus, usually we must start the search and evaluation of the parasites almost from the beginning. According to our studies, whose results are dealt with in the distribution chapter of this book, the search for parasites should be started with the evaluation of pest distribution with respect to separate floristic zones, as the parasites are dependent in their distribution on these zones and associated aphid fauna. It is necessary to know, at least generally, the area of the home of the pest, which is kept as the basis for further research. In case that the aphid is attacked by any aphidiid parasites, it will almost surely be attacked by some species in the area of its origin. Therefore, the parasites that attack the aphid in its home are one possible source of parasites where these should be searched for. This is also the commonly accepted praxis. But this source is not the only source of parasites. The aphids often spread over considerable distances either naturally or through man's action (accidental introduction) and they consequently occur in a number of other floristic zones, i.e. in other environments besides their original home. The classification of the distribution area of the aphid in accordance with separate floristic zones and associated faunistic complexes of parasites allows us to derive the districts in which the aphid is actually (literary records) or is expected to be attacked by members of the corresponding faunistic complexes; it is well known that the members of these complexes can be considerably effective in the limitation of the immigrating aphid species (e.g. *Lysiphlebus testaceipes* and *Toxoptera aurantii* in Cuba). Thus, areas of separate faunistic complexes in which the aphid occurs repre-



Fig. 309. *Hyalopterus pruni* on *Prunus domestica*, outbreak. Czechoslovakia. Above: damage caused to leaves. Below: damage caused to young fruits.

sent another source where the parasites should be searched for as well. Parasites associated with aphid species which are related taxonomically or ecologically (variants, etc.) to the given pest should also be searched for, as they could be useful in control, too.

We have mentioned the general principles of collecting the parasites in the introductory chapter. In every case, a general knowledge is necessary and a less experienced collector should seek advice at corresponding instances, together with advice on methods, collecting equipment, preservation and shipment of the collected material. Usually, we collect parasites attacking a certain aphid which is the object of control in another country, the given species then being the leading object. However, we try to recognize the hosts of the parasites by collecting some other aphids and we collect also other parasites whose host specificity range could be useful. The samples are taken in all the environments, both in wild and cultivated ones, in which the aphid occurs in the studied area and, as far as possible, throughout the whole season. For introduction purposes, it seems preferable to collect aphid colonies that are seemingly not parasitized or include a relatively low number of mummified aphids and to rear them in the laboratory, while the presence of almost single aphid mummies mostly means that the aphids had emigrated from the colony and at this period



Fig. 310 Natural limitation of *Hyalopterus pruni* on leaves of *Prunus persica* by indigenous parasites. Italy. Above: *Praon volucre* and *Ephedrus plagiator*. Below: *Aphidius transcaspicus*.

a great part of the mummies is usually hyperparasitized (Figs. 309, 310). Photographs of the habitats, aphid and parasite microenvironment, general and detailed pictures of aphid colonies, are a rather valuable complement to the information of the collector and may be rather useful during the release in the country of introduction.

According to BARTLETT & V. D. BOSCH (1964), in a foreign country the search for a pest and its natural enemies need not be conducted upon native vegetation in relatively inaccessible areas, as experience has shown that botanical gardens, parks, experimental plantings, domestic gardens, national forests, ornamental vegetation along walkways and roads, and similar accessible planting or non-cultivated vegetation will generally support populations of the insect being sought.

Our opinion is that the research must be started first on the basis of natural environments because of the following reasons: an indigenous aphid, if it is a pest in its native home or not is primarily connected with natural environments, which are primary as to their development. Consequently, natural environments, which are heterogeneity must be the base of search where the aphid original environment and associated parasites are found. Only this kind of research can show us the true

requirements of the pest and parasites and help us to understand its distribution in the cultivated districts. As the parasites are primarily connected with certain floristic zones in their distribution, these natural zones in which the pest occurs should be studied first and research of cultivated lands should follow later. Naturally, there is no doubt that it is much easier to search for the host as well as for the parasites in the cultivated or semicultivated environments mentioned above, where a number of aphids are known to be concentrated, but except for the incomplete data on the aphid and parasite distribution we should not obtain any observation on true ecological requirements of the organisms studied. Thus, according to our opinion, the first necessity is to obtain some general information on the floristic zones of the area, study them methodically to recognize the relations of the organisms studied in these communities, and to relate these records to later research in cultivated lands.

Selection of species for introduction can be undertaken from various points of view. Usually, there is a certain restriction of the theoretical requirements through the practical possibilities such as obtaining of the material from various areas of the world and information on it in its native country.

It seems that we are mostly restricted to such records as those about the climatic area, habitat and host, while more detailed records seem to be rare. Thus, we can agree with V. D. BOSCH et al. (1964) in that preselection studies are influenced by expensive and time-consuming research of the parasites in their home, while the main significance are the post-introduction studies undertaken in the country of introduction. This trend has been successfully followed and it is obvious how complicated such a research is, even if undertaken in the introduction country, and that this would not be possible in various parts of the world where the search for parasites is undertaken. Naturally, some records on the effectiveness of a species in its native country may be rather stimulative, but it is necessary to keep in mind that effectiveness is only a relative phenomenon, which is greatly influenced by the changeable environment, on the other hand, the species which is rare or poorly effective in its home can become more effective in new environments.

Climatic similarity is a general phenomenon according to which the species or strains are selected. North-south introduction or introduction in climatically similar belts is recommended, but even here some field records show that the species sometimes do not behave in the way expected because of their origin. For example, parasites of *Therioaphis trysilii*, which were introduced into California, become distributed in similar environments as in their native country as was predicted prior to introduction when the material of parasites was searched for (see: V. D. BOSCH et al., 1959, 1964, etc.). On the contrary, the records on the distribution of *Aphidius smithi* in the Nearctic America, besides the climatically favourable areas in which it was expected to establish, show that it has spread considerably northwards and occurs in areas which would seem to be too cool for a species of Indian origin.

Another viewpoint on the selection is the number of species to be introduced and whether monophagous or widely specialized species are preferable; further, whether we should transfer the natural food chains into new environments or develop a new mixture of species, which are introduced from various areas and are expected to develop as a complex in the new environment. This problem is rather complex, but the general idea of the approach should be to follow the ideal natural state, where the host organism is limited in all the environments in which it occurs (multilateral limitation). This may be done by one or more species, by a monophagous or widely specialized enemy. The natural state of the composition of parasite complexes (and other natural enemies) of the aphids shows that there is a clear preference for the limitation of an aphid by a complex of parasites (natural enemies) which replace each

other in action. This state of specific heterogeneity in the composition of parasite complexes strongly supports the stability of the ecosystem.

The above mentioned theoretical approach naturally must be modified in dependence on the host species and its occurrence in various environments. In selecting the species we must keep in mind that both the pest and the introduced enemies will never occur in the really same environment as they could do in their native country, as mentioned earlier. Besides other factors of the environment, the indigenous natural enemies in the country of introduction will take their part in the limitation of the pest, so that the introduced natural enemies will naturally become members of at least partial artificial food chains. In the control of a pest, our main idea is to control the pest both in space and time in the given environment and we may use as many biotic agents as necessary to follow this approach. Although we deal with this in a separate chapter (multilateral control) it is necessary to stress the basic feature of the approach to pest aphid control—in that although a pest is controlled mainly in a given crop to be protected from injury and to preserve the greatest part of the harvest for man, we must not forget that its sources may occur, and mostly do so, in other environments, from which they disperse and attack the crop. Thus in selection of species, we should select also the species which are expected to attack the pest also in other environments as well as in the crop, or in the other environments exclusively; this can happen accidentally when the parasites occur in the same environments as the pest, or the control activity of man must cover also this field of action. Usually, as the praxis of control of various aphids shows, we are successful in controlling the aphid in certain environments or microenvironments, while certain gaps occur due to the lack of parasite coincidence in occurrence; this is often due to lack of alternative hosts, specific requirements of the parasites on the microenvironments, etc. To cover these gaps in control, it is possible to introduce better adapted parasite species or strains. However, as it will be later shown (integrated control), complete biological control, although required, is rare and the existing gaps in pest control are compensated by other means (selective insecticide treatments, etc.).

—SHIPMENT. There is no doubt that a laboratory stock, when reared under favourable conditions, is the best to use as a source of shipped material. Large research institutes possess various semipermanent laboratories, which permit the rearing of collected parasite material in pure cultures before it is sent to the country of introduction. These semipermanent laboratories have another still more important significance: in many cases, the handling of a parasite is not developed until the material is introduced. Such conditions are a risk, as unfavourable conditions may result in the elimination of the introduced stock. The possibility of rearing a parasite under laboratory conditions in the country of its origin allows us to establish at least the main requirements of the parasite on the environment and this knowledge is a valuable part of the sender's information which can be used in the country of introduction. In semipermanent laboratories, too, we are able to obtain another stock from nature in case that certain laboratory conditions were unfavourable and a stock was eliminated as a result. These advantages are rather obvious so that in every case it is recommendable to use this method of work. In the case that there are no semipermanent laboratories, it is mostly advantageous to ask the local authorities and temporarily use their rearing laboratories.

In many cases, however, there is not even this possibility and the field collected material must be shipped. It is advisable to collect the material which will include mostly mummified aphids because of shipment, in larger quantities, as a certain part of the material is usually hyperparasitized and there is a certain mortality among the mummified parasites en route. As mentioned above, we must start the rearing of a

parasite in quite an original and partially risky way in the country of introduction in consequence.

Generally, we ship three kinds of parasite developmental stages: (1) Parasite eggs and larvae that occur inside living aphids; (2) last instar larvae, prepupae or pupae of parasites that occur inside dead mummified aphids; (3) parasite adults. It is obvious that the most disadvantageous is the first kind, as it requires, on the one hand, the simultaneous transport of a green plant as a source of food for the shipped (partially) parasitized aphids, on the other hand, we ship simultaneously a new stock of the pest to the country of introduction. Thus, such material is perhaps useful for consigning very short distances as it allows the plant or its pieces to be fresh, not to evaporate and not become rotten; short distance shipping, too, does not always mean an eventual introduction of new stock of the pest. The second and third kinds of parasite material cannot be strictly separated from each other: we ship mummies but usually a certain part of the parasites emerge so that both mummified aphids and living parasite adults are received at the place of introduction. The sending of mummies is the best method. The developmental stages of parasites inside these mummies appear to be most resistant to adverse environmental conditions which could occur during shipment as they do not need any food or water en route; however, we must keep in mind that the parasite adults which emerge need at least honey as food (see: methods).

There are two points of view on the number of specimens sent in a consignment. First, it depends on the possibilities of the collector how many parasitized aphids he had found and was able to ship in time, whether the material is field-collected or laboratory reared, etc. Naturally, the more material sent, the better for the receiver. However, even a relatively small shipment may be enough for the establishment of a laboratory stock. For example, the original number of *Aphidius smithi* shipped from India to the New Jersey insectary was 110 mummified aphids, which provided 17 ♀♀ for use in the propagation work, and during the following two years more than 74,000 specimens were produced in the insectariums (ANGALET & COLES, 1966). Similarly, we obtained numerous progeny of *Aphidius megourae* from the original number of about 10 mummified *Megoura viciae* which were shipped to Czechoslovakia (STARY 1964).

Secondly, the number of specimens sent in one shipment depends on the purpose for which they are required. A relatively small number of specimens is enough for the establishment of a laboratory stock in another research institute, while this number must be considerably more numerous in the case that the material shipped is directly to be released on a new site. In any event, we must keep in mind that a certain mortality occurs among the material during transport (Table 15).

Although the shipping conditions may be favourable throughout the year, there are certain factors that restrict the shipment to certain periods of the season. Because of transport velocity, we should avoid periods of heavy traffic (Christmas period, etc.). Similarly, extreme temperatures that occur in certain periods of the year in some countries should be avoided. Further, there must be some preliminary cooperation with the receiver to prepare the laboratory conditions, namely to rear the host plants and host colonies to establish the introduced material in the quarantine laboratory. This work of the receiver will take some time and it is not possible in certain periods of the season to obtain host plants and host aphid material. All this must be planned well in advance.

Although modern transport is very quick, there are differences between inter-continental distances and distances inside a smaller country. The distance may partially influence transport methods. When the material is sent to shorter distances,

Species	No. of shipments	No. of parasites		Survival (%)
		Shipped	Survived	
<i>A. semiflavus</i>	7	15,840	14,331	90.0
<i>Pr. palitans</i>	10	17,750	15,711	88.5
<i>Tr. utilis</i>	24	15,185	13,768	90.6
Total and average		48,775	43,810	89.8

Table 15. Survival of adult parasites of *Therioaphis trifolii* following shipments to the release area near Tempe, Arizona, 1956-1957: *Aphelinus semiflavus*, *Praon exoletum* (= *palitans*), *Trioxys complanatus* (= *utilis*) (BARNES, 1960).

we can even send pieces of green plants infested by parasitized aphids, a small water supply being added (see: methods), while this is not possible in long-distance shipments.

Shipment methods in biological control are very heterogeneous and are rather influenced by the material itself. In aphid parasites, which exhibit comparatively the same biological features, they are relatively very easy, however, even here we must accomplish certain requirements as to the parasite survival during shipping, quarantine procedures, etc.

A shipment container may be subdivided into three layers: the first layer is the external container, then an inter-layer follows, which is placed around the inner container.

External shipment container. It should not be heavy, it must be strong in construction to prevent damage to the inner container during shipment, it must prevent the eventual escape of the living material, and it must at least partially prevent the influence of changes in temperature of the external environment affecting the shipped material. Light metallic or compressed paper or plastic containers seem to be the most suitable. They may be even combined: a light metallic or paper container is useful in preventing damage, while certain plastic materials keep a relatively constant temperature inside (see: release). These external containers bear the address labels of the sender and receiver as well as printed caution labels. (Figs. 311-312).

Cloth sacks. These resemble an envelope in which the inner container is transported. They prevent the strong movements of the inner container during transport, but their main function is to prevent the eventual escape of the shipped material from the inner container (Fig. 311).

Inner shipment container. It contains the shipped parasite material. Its dimensions are somewhat different depending on the stage of the material shipped. Mummified aphids may be sent in small boxes, in which there is mesh netting to prevent movements and possible injury to mummies. We put some small droplets of honey on the walls of the box as food for parasite adults that may emerge during the transport (Fig. 311). Adults of parasites are sent in large paper containers the inside of which contains wood wool to provide resting sites for the adults; droplets or strips of honey are on the walls of the container as a supply of adult food (Fig. 311).

We have found somewhat modified plastic bottles to be rather useful for the shipping of parasite material over shorter distances: the inner portion of the cork is cut and a piece of nylon texture is placed there instead, then a small vial containing honey or honey-water is closed by a piece of cotton wool and over the whole cork another layer of nylon texture is placed and tied with rubber; a cloth sack may not be necessary then.



Fig. 311. A - container, B - small plastic box with a net inside to prevent the extreme movements of mummified aphids sent, C - 2 small bags, which have to prevent the eventual escape of insects. University of California, Riverside. Used for sending *Aphidius smithi* mummies.

Fig. 312. Container used for sending aphid mummies and adult parasites. University of California, Riverside.

The Sender must first send an advisory note to the Receiver about the material prior to shipment to allow him to prepare the laboratory rearings and inform the quarantine officers. Then, a brief report is added to these shipped materials (data about shipment and packaging, host insect, parasite species, host plant, collection locality and date, name of the collector) while more detailed data on host specificity, etc., which are important for later phases of biological control program, are sent under separate cover, if necessary.

The Receiver must arrange with the quarantine authorities, air-line and post officials to be immediately informed of the arrival of the shipped material. The receipt of the material must naturally be planned in accordance with the Senders suggestion so that the corresponding equipment in the quarantine and biological control laboratory is prepared. Sufficient rearing stocks of host aphids on suitable plants are the main task. If several stocks of the parasites are sent, they must be selected during and after the quarantine state of research. After the material is transferred to the quarantine laboratory and eventually reared for several days to allow the parasite to oviposit, etc., the Receiver sends his report to the Sender (date of receive, condition of the shipment, etc.).

- QUARANTINE LABORATORY. Quarantine handling of entomophagous species that are imported into a given country should be so organized as to prevent simultaneous introduction of undesirable species both of plants and animals. We must keep in mind that, although beneficial organisms are introduced, the consignments can include the natural enemies of these beneficial insects or another different population of the pest.

Quarantine requirements need the propagation of an introduced parasite species for at least one generation under quarantine conditions.

Quarantine facilities and procedures to biological control projects are a rather important part of the program. They have been dealt with satisfactorily by Risuta (1964) so that they are mentioned only very briefly in our book: aphid parasites

represent a comparatively very simple problem in many ways, but, the quarantine phase of a biological control program may not be omitted.

Any received shipment must immediately be transferred to the quarantine laboratory and further activities—from the opening of the parcel to the transferring of the parasites to quarantine rearings, and the sterilization of package for later burning of the container—must be done with scrupulous quarantine care.

Each sample received must be put in a separate isolation cage to prevent a mixture of separate strains or even species of parasites.

Both in the quarantine and biological control laboratory the optimum temperature and humidity requirements for aphidiid parasites are generally agreed to be approximately $+18^{\circ}\text{C} - +24^{\circ}\text{C}$ and 50–70% R.H. Naturally, these conditions may be changed with respect to the specific requirements of separate species. Care should be taken to see that the same temperature is really optimal for both host and parasite. It has been generally recognized that there are aphid and parasite species that require lower or higher temperatures (see: rearings).

The continuous rearing of aphids and parasites in separate cages does not represent a peculiar problem. It is necessary only to add new host aphids and plants, and a few drops of honey as food for parasite adults; periodical watering is also recommended. We have found it to be a suitable method to grow the plants in smaller containers, new plants being gradually added and old ones removed so that a continuous source of aphid host plants is secured. If the cage is smaller and the older containers or pots with old plants and those injured by aphid feeding must be removed, the upper portion of the plants are cut and left inside the cage, while the containers are removed; this is necessary as the mummified aphids may be found on older plants, on the other hand, a chance must be given to the living aphids to disperse from the old to new plants.

Mating of parasites need not be dealt with as both ♂♂ and ♀♀ emerge from mummified aphids; sex ratio may be important in continuous rearings but does not seem to have importance in quarantine isolation.

Host instar preference can be recognized from the mummies obtained through shipment. Usually, lower instar aphids are attacked by parasite ♀♀.

Care must be taken in searching for emerged hyperparasites, which should be immediately collected and removed from the rearing cage. In case that hyperparasites were established it is recommendable to rear the received material for a further 2–3 generations in the quarantine laboratory as the hyperparasites may not be collected in time and they may succeed thus to deposit some eggs. The hyperparasites are easily recognizable, differing both in general habitus and behaviour from the primary parasites.

Quiescent states do not seem to cause any trouble during the transport of the parasites as mostly non-quiescent cocoons can be found in the field, furthermore, air transport is rapid so that the eventual influence of certain temperatures on parasite adults is short. Nevertheless, care must be taken to maintain the temperature optimum in the rearings as temperature may induce facultative diapause in some species of parasites (see: seasonal history chapter).

All the data obtained during the quarantine period of a biological control program are carefully collected and are then put at the disposal of the biological control laboratory worker.

A part of the material reared in quarantine, after the adults die or when the rearing becomes more numerous, must be mounted and correspondingly labeled with all the necessary records and preserved for eventual later taxonomic identification or revision.

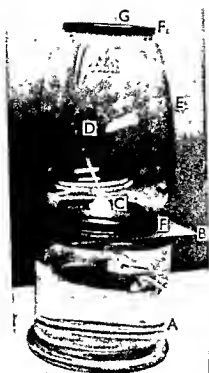


Fig. 313. Rearing methods. A - glass container with water, B - plastic plate with central hole, C - cotton wool to fix the plant in the hole, D - plant with aphids, etc., E - glass container opened at both ends, F - rubber, G - nylon texture.

In general, at least in aphid parasites, it seems that the most ideal conditions would be for all this work, both quarantine and basic laboratory work to be undertaken by the same worker or staff, who knows also the hardly definable minute peculiarities in the biology of the introduced species. For this reason, we have included the quarantine laboratory as a part of the biological control laboratory. Naturally, such a skilled research worker or team must have several years' experience with the rearing of various parasites, so as to recognize all the minute details in their requirements on the environment.

- BIOLOGICAL CONTROL LABORATORY. Prior to starting mass-rearing activities, we must have some laboratory information on the introduced parasite. For this purpose, we have continuous caged pure cultures of host and host plus parasite, from which the material for other experiments is taken. Nylon texture covered cages of 35×35 cm or 35×70 cm are rather useful. Pure cultures must simultaneously occur in several cages to prevent, for various reasons, an unexpected elimination of the stock. Potted plants are useful or we may grow the plants in nutrient solutions or other media. We have successfully used *Vicia faba* seedlings grown from seeds in wet sawdust (Fig. 314). The cages must be watered, and air circulation is necessary. A few drops or narrow strips of honey can be put on the walls of the cages or on the plants as a source of laboratory food for parasite adults. Either fluctuating or (optimum) constant temperatures may be used. In the second case, we must be careful, as in some cases the optimum temperature for the host may induce diapause in the parasite.

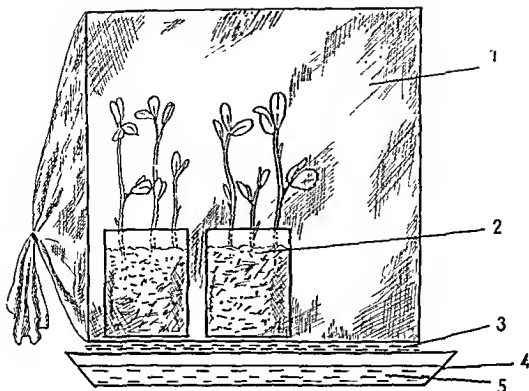


Fig. 314. Rearing silon (= nylon) cage for breeding aphids and parasites in the laboratory. 1 - silon texture, 2 - bottles with bean plants, 3 - wire netting, 4 - plastic pan, 5 - water (STARY, 1966).

Average temperature conditions in rearings depend on the aphid species. Some aphids, as mentioned also by FISHER (1964), require cooler environments (e.g. *Aphis fabae*, *Acyrtosiphon pisum*, *Aphis spiraeicola*, *Toxoptera anrantii*), while other species prefer higher temperatures (*Aphis craccivora*, *Megoura viciae*, *Therioaphis trifolii*, *Aphis gossypii*, etc.). It is advantageous to rear each host species and associated parasites in a separate small room to prevent mixed cultures, which can occur when several host aphids are reared on the same species of host plants in the same room. Host specificity of aphids can be useful to allow some species to be reared in the same room without the danger of accidental mixture of cultures, while other species must be separated. The obviously best average temperature, at least for the initial stage of the research, is $+18 - 24^{\circ}\text{C}$. Fluorescent or day-light can be used. Light period must be controlled to preserve the parthenogenetic reproduction of aphids. Detailed observation on parasite oviposition, mating behaviour, etc., is usually performed in Petri-dishes or in isolated containers (Fig. 313). For this reason, colonies of aphids are reared on leaves of plants put in water (BROUSSAL 1966, HAFEZ 1961), or leaf-discs floating on culture solutions are reported to be useful (HUGHES & WOLCOCK 1965). Young seedlings grown from seeds are also good for aphid rearing and detailed observation. Actual fecundity of parasites may be established by transferring the ♀ parasites each in a smaller cage with aphid infested plants.

Generally, the aphidid parasites are not difficult material to rear successfully in the laboratory. They usually mate soon after emergence so that there is no danger of lack of mating in laboratory rearings as mentioned in other entomophagous insects. Naturally, there are many specific features in parasite biology which can be

established by an experienced worker, as this is true for all the groups of entomophagous insects. Density of host and parasite populations must be observed, periodically the aphids should be added or the supernumerary parasites removed.

It seems advantageous to first elaborate a brief review on parasite biology to enable the mass-rearing program to begin, while further detailed observations on parasite biology, host and parasite relations, etc., may be dealt with simultaneously with the mass-rearing production. There is no doubt that field experiments and problems that arise during the parasite establishment in the field give us a rather rich and continuous source of problems.

— *Evaluation of results.* On the basis of the laboratory information obtained we may at least preliminarily select the parasite species. Temperature requirements of separate species will probably be the first criterion necessary for the elaboration of the plan of release sites. Host instar preference will give important information on the mode of parasite spread. This basic information must be completed by records received or obtained in the native home of the parasite (habitar, host specificity range, etc.).

BARTLETT & V. D. BOSCH (1964) summarized the viewpoints of various authors in that there are two schools: one school of thought has maintained that where several natural enemy species attacking the same host were considered for import, only one species having the best predetermined attributes should be introduced, while the opposing view holds that all natural enemy species should be imported and colonized.

In our opinion, we should follow the natural conditions, where the action of the natural enemy is characterized by a complex action of several species which attack the host in different environments and microenvironments and replace each other in action. The truly ecological homologues seem to be rare in nature, while the greater heterogeneity of the parasite spectrum seems to cover the possibly occurring gaps in aphid limitation more favourably.

— *Mass-production.* 1. Mass-rearing of parasites is a part of a chain of procedures, which consists of the mass-growing of aphid host plants, mass-rearing of aphids on these plants, and mass-rearing of parasites on the aphids.

The plants can be cultured in pots with soil, or grown in nutrient solutions. Because of the necessity of light, it seems to be preferable to cultivate the plants in a greenhouse, and transfer them from there into rearing rooms for future use. Strip organization of the plants in rearings is useful, i.e. pots with plants of the same age are situated in the same strip, and the separate strips containing plants of the same age are then exchanged and replaced, the senescent plants are removed and replaced by young ones, etc., there being a continuous chain of young, middle-aged and senescent plants in the rearings. This system is rather advantageous as the aphids can migrate from the old senescent plants to the young ones.

Aphids and parasites are reared in propagation cages or units. We agree with FINNEY & FISHER (1964) in that smaller units are more favourable as they enable closer control over the cultures and also the elimination of eventual contamination is easier. Rearing cages can be situated in rearing rooms under fluorescent light or in a heated greenhouse. Controlled temperature, light, and photoperiod is necessary, together with air circulation and watering. It is still a problem as to whether constant or fluctuating temperatures should be used in the rearings. Rearing rooms have many advantages, especially as there is less probability of contamination of rearings by hyperparasites and the conditions can be controlled more easily and precisely. Greenhouses seem to be most advantageous for the growing of plant material. They can be used as rearing rooms probably successfully only from late autumn to early spring in a temperate zone, i.e. during the period when the external conditions do not enable the occurrence of hyperparasites and other natural enemies. Host and

parasite density in rearings must be controlled to give the best results. It is recommendable to add honey as food of parasite adults.

In the rearings, we use either the pest as the host aphid or alternative or even unnatural hosts may be favourable especially when the pest can be cultured only under difficulties. For example, we have successfully used *Aphis craccivora* as an unnatural host of *Aphidius trawscaspicus* in the rearings, as the original host, *Hyalopterus pruni*, was difficult to rear. Mass-rearing of parasites on unnatural foods is another problem. Direct culturing of parasites on artificial diets does not seem to be suitable for the aphidiids. Very few successful cases of breeding hymenopterous parasites on artificial diets are known. As to the aphidiids, we are rather sceptical as the following features will hardly allow a successful application of a similar rearing method: oviposition (oviposition behaviour), larval development (relation to various tissues), pupation (aphid skin is mostly needed), emergence of parasites. Culturing of parasites on hosts bred on artificial diets could be perhaps useful for mass-rearing of aphid material. The rearing of aphids on artificial diets has been mentioned by several authors (see: MITTLER 1958, etc.), but it still remains a question whether the rearing of aphids on plants is not more advantageous. Culture methods for mass-production are of three types: periodic contact, limited contact, and continuous contact (see: FLANDERS 1954).

2. Mass-collection of parasites can be undertaken by the following methods:

Aspiration. For parasite individuals a commonly used mouth-suction collector is quite useful; do not forget, however, to put a piece of nylon texture inside to prevent mechanical injury to the parasites when they are sucked in. For mass-collection, however, an aspirator-suction-collector is better; the material was collected into plastic bottles, which were later covered by nylon texture and closed with an adapted cork. In these bottles, too, the parasites were stored and transported to release sites (Figs. 315).

Anaesthetization. Anaesthetization of parasites by CO₂ sometimes in combination with ether (see: FISHER & FINNEY 1964) has been used by various authors. In our opinion, this method is not necessary in the case of aphidiids, as the parasites can easily be collected by aspiration when utilizing their phototaxis. The above mentioned method might perhaps be used when counting the adult parasites, nevertheless, cold storage conditions seem to decrease the motility of adults to a suitable degree, this being simultaneously an easier approach to the matter. Anaesthetization may have also adverse effects on the material (see: WIACKOWSKI 1960, 1962).

Utilization of parasite taxes. Positive phototaxis is most useful in parasite collection. The adults may be easily collected on the ceiling of the rearing cages, or on specially adapted windows.

Collection of the material via utilization of their taxes must be timed. The parasites accumulate on ceilings when being disturbed by slight mechanical movements of the plants, the same as when they are searching for water; similarly, their accumulation seems to be greater in the case of higher temperature and relative lack of water in the rearings. Therefore, we collect the parasites prior to watering the cages.

As already mentioned, counting of the material is necessary prior to mass-release of parasites. When releasing adult parasites, the containers with collected material must be placed for a short time in lower temperature conditions (about +8 - +10°C), or the adults are anaesthetized by CO₂. When mummified aphids on plant stems are released, the stem- or leaf-counting methods can be used.

3. Preparation of artificial foci units was developed during an experimental program of introduction of a parasite of *Hyalopterus pruni* into Czechoslovakia, but it was later found useful also for mass-production and release of some other introduced



Fig. 315. Mass-collection methods. A - plastic bottle, B - suction collector cork, C - plastic cork with cut out central portion, D - plastic funnel, E - rubber hose, F - aspirator, G - closed plastic bottle with parasite material, H - nylon texture.

parasites. The principle of the method is very simple: we use the wooden boxes which are commonly used for the transport of vegetables or fruits, as rearing containers. A layer of soil is put into these cages, and seedlings of the host plants are grown there. Later on, the young plants are infested by aphids which are then exposed to parasite attack. After a day or two, long enough for parasites to attack a number of aphids, the artificial foci units (AFU) are transported to the field and left in release sites, where they serve as artificial foci, where parasites can find their hosts and spread from there to the surroundings. The AFUs may be prepared either in a greenhouse or in a rearing room. Either natural, alternative or unnatural hosts can be used as the host aphids in these units. AFUs cannot be stored for a longer time because of plant growing and resulting trouble during transport, so that timing of AFUs production is necessary.

4. Semifield and field rearings. Large cages may be situated in semifield or field conditions for the purpose of parasite mass-production. The natural conditions, when favourable, are practically a rather useful laboratory, although there is danger of contamination of such rearings by hyperparasites and other natural enemies. These confined rearings are useful because of the easy growing of plants. Sometimes, it is advantageous to add pure cultures of aphids into the cages to increase the density

of populations in them. This method was successfully applied by v. D. BOSCH et al. (1959) in experiments on initial establishment of introduced parasites of *Therioaphis trifolii* in California. We used the same method of rearing in initial establishment experiments on parasites of *Hyalopterus pruni* in Czechoslovakia.

Mass-production of parasites can take place in permanent establishment plots of parasites in field conditions. Special methods were developed to collect such material for release purposes (see below).

— FIELD WORK. CLAUSEN (1936) has perfectly summarized the relations between the laboratory and field work in biological control: successful rearing under controlled laboratory conditions however encouraging, gives little assurance of establishment in a more rigorous field environment.

In a biological control program we commence with field observations on the occurrence and action of various parasites. Then we collect them and send them to the laboratory. We deal with them here and then introduce them to the field, although in more or less other conditions. We understand some features of their biology in the new environment very poorly, so that we again make experiments in the laboratory, etc. Thus, if we classify the laboratory and field work in biological control, there is no doubt they both are very complex.

— Colonization. Colonization is a phase of the biological control program in which we translocate the introduced organism into the field conditions of a new country. This is a rather responsible phase of the program, as we must transfer the material from the laboratory conditions to the field, select a favourable site, release the parasite at a suitable time and in certain numbers. It is obvious that the released parasites can be influenced by a number of factors, which could be adverse or fatal to them, and it is just the aim of the colonization procedure to diminish these risks and to try to select the best new environment for the introduced parasite.

— Colonization site — 1. Number. It is a generally accepted opinion in biological control praxis that it is best to liberate the limited number of natural enemies all in the same place and at the same time rather than to distribute them in a more sparse population over a wider area. The application of this principle is influenced by the quantity of material available and by the release method. There is no doubt that confined release requires relatively less material and we can start the confined release experiments at several places simultaneously, while open release generally needs a higher release number concentrated on one plot.

As correctly stressed by DEBACH & BARTLETT (1964), the initial release of a new species should be made to cover as diverse a climatic area as is practical so that the most suitable environment will be encountered; since it is relatively impossible to foretell exactly how a species will react to a new environment, the common procedure in colonization is to set up a reasonable number of liberation sites with varied environmental conditions and concentrate the initial release to these locations.

(a) Temporary and permanent colonization sites. We may release the material in a random manner in a suitable stand, or select a permanent colonization site. For example, v. D. BOSCH et al. (1959), in the initial stages of the *Therioaphis trifolii* parasite introduction program, released a relatively small number of parasites indiscriminately on commerce alfalfa fields in southern and northern California; despite a numerous release of this type on heavy aphid infestations, no recovery of parasites followed after several months. On the contrary, establishment of parasites was achieved on permanent colonization plots, where the same plots were colonized repeatedly. However, even temporary colonization may be successful as shown by results of the introduction of *Aphidius smithi* in Hawaii (see: Ann. report, 1960–61). There is no doubt that a selection of a permanent colonization site allows a better possibility

to eliminate the influence of adverse factors such as insecticidal treatment, etc.

(b) Natural and cultivated stands. It seems to be quite certain when an introduced parasite has to become permanently established it should occur both in natural and in cultivated stands, because natural or seminatural habitats form the frame of cultivated land. There is, of course, no strict separation of natural and cultivated stands as a number of ecotones as well as mixed stands occur. From this point of view, it would perhaps be better to classify the parasite occurrence in a given area as being in unstable or stable stands, as the latter include both natural and cultivated habitats. We must keep in mind that even some cultivated crop fields can represent a relatively stable environment. For example, just the generally known examples of biological control of alfalfa aphids in California represent a case, when the introduced parasites were established permanently on the alfalfa fields, but there are no records on their occurrence (foci) in roadsides, waste lands, etc. We believe that both aphids and parasites can occur in such places as well, although being restricted to a single host, as alfalfa plants are commonly encountered outside the fields. However, even if the parasites occurred only on alfalfa fields, the character of the stand—the life cycle of the host aphids as well as the perennial character of the community—is favourable for their establishment; the parasites, which are originally or through environmental modification strictly specialized to their on alfalfa occurring hosts, may overwinter in the alfalfa fields and also survive the hot adverse summer conditions, at least to a greater extent of the California districts (cf. v. D. BOSCH et al. 1959, 1964). This would not be the case of an annual crop, which is attacked by aphids only seasonally and moreover, annual crop fields are strongly influenced by agricultural practices (ploughing).

This problem is more complicated in connection with the origin of the pest, its occurrence in natural and cultivated ecosystems, adaptation of indigenous natural enemies and their action during the season, etc.

2. Criteria. (a) Character of the stand. As already mentioned, the colonization site must show at least a certain stability; stable environments should have preference. As the aphids are seasonal inhabitants of annual crops, the parasites cannot occur perennially in such a stand; then there is the problem of whether they are able to disperse and follow the host to another habitat (climate zone influence) or not. In any case, the selection of annual crop fields (unstable stand) is risky. We can illustrate this with several examples: In Cuba, *Aphis craccivora* is a common pest of vegetables grown in fields, but it occurs on quite a number of other crops and plants, in almost all the habitats over the island; however, in annual crops—e.g. beans—it occurs for a short period, while in other stands—e.g. on way-side trees (*Gliricidia*)—it stays much longer; the latter plants too are often found in rather heterogeneous habitats, being grown all over the island. *Lysiphlebus testaceipes*, which is an indigenous parasite of this aphid in Cuba, parasitizes the aphid heavily on *Gliricidia* trees, but we found poor or no parasitization in young bean fields; this is obviously a result of the annual community character of a bean field as well as a matter of aphid and parasite dispersal. In the case that we should introduce another parasite into Cuba to control the aphid, there is no doubt that it should be released in stands where *Gliricidia* trees infested by the aphid are common, there would occur certain, perhaps partially adverse, relations of an interspecific character between the parasite species, but they both could occur simultaneously as a certain percentage of aphids remains free of parasites under *Lysiphlebus testaceipes* action. Or, another example from C. Europe *Acyrtosiphon pisum* is a common pest on alfalfa, which is a perennial crop, however, during the season, a part of the aphid population migrates and attacks annual leguminous crops such as common beans, peas, etc., but as soon as

these crops become fully grown and thus unsuitable for aphids, the aphids emigrate to perennial crops. It is obvious that *Aphidius smithi*, during the introduction program, should be released on alfalfa fields, while the success of this release on peas and beans would be adversely influenced by the life-cycle of the aphid and character of the stand.

(b) Aphid life-cycle and population density. When the parasite is introduced into a release site, there must be a relatively high host density to enable it to reproduce successfully. However, it is well known, that host population density in a certain plot fluctuates, the aphids can emigrate partially or completely from a certain stand, etc. As the perennial host's presence is important in a parasite release program, we must classify the host life-cycle and corresponding changes in host densities in the given release site. In connection with corresponding peculiarities there are various differences in individual climatic zones (see seasonal history chapter). For instance, dioecious aphids in the temperate zone alternate the type of habitat in connection with obligatory migrations; this means that the introduced parasite, which is basically habitat dependent, cannot survive the temporary host absence if it is not able to find some alternative hosts or to enter the diapause. According to our studies, we can develop artificially some "mixed" stands in intermediate habitats, where both the primary and secondary host plants occur together: this enables the parasite to find its hosts throughout the whole season at the same place. Similar mixed stands may also be found and selected under field conditions. We have used such an artificial stand when colonizing *Aphidius trautsciacus*, a parasite of *Hyalopecterus pruni*, in Czechoslovakia: *Phragmites communis*, which is a secondary host plant, was potted and grown under *Prunus domestica* trees which is the primary host plant of the aphid. This procedure was followed in an initial establishment program, as the host migration was one of the reasons why the parasite failed to establish in several release sites. Another example of the significance of host life-cycle with respect to a parasite colonization site may be mentioned from the tropics (Cuba): *Aphis spiraeicola*, though attacked by the indigenous *Lysiphlebus testaceipes*, is an object of possible biological control in Cuba, where another parasite species should be introduced. The aphid is a pest of Citrus especially, but can be found on various plants over the island. It is parthenogenetic in the tropical conditions of Cuba, and migrates from one plant to another throughout the year; thus, as Citrus is suitable as its host during a part of the season only, the aphid is its seasonal pest. The selection of a citrus orchard as a parasite colonization site would be incorrect, as the parasite would not find the host when the aphid emigrates from the orchard. Therefore, in the initial colonization stage, it is recommended to colonize an introduced parasite species in mixed stands such as irrigated gardens, where some plants are always suitable for the aphid and it is perennially present there.

(c) Indigenous natural enemies. If we have to control an introduced pest which is attacked by indigenous natural enemies, there is a probability of interference of indigenous enemies with the action of the introduced parasite, the problem is still more acute if we have to control indigenous pests with introduced parasites. However, where the indigenous natural enemies have become adapted to the pest, they will probably hinder the establishment of the initial parasite population. Such observations were made in California (*Therioaphis trifolii* parasites, V. D. BOSCH 1959, 1964, etc.: *Chronaphis juglandicola*, SLUSS & HAGEN 1966). A still more obvious case is that where we introduce a parasite to a community where there already exists a native parasite effective in a part of the season and we plan to cover the existing gap in aphid limitation by the action of an introduced parasite. This was, for example, the introduction of *Aphidius smithi* into Czechoslovakia, where the native parasite, *Aphi-*

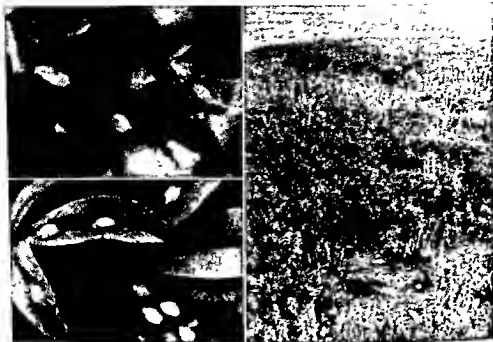


Fig. 316. *Acyrthosiphon pisum*, a heavy infestation of alfalfa and limitation of the aphid by *Aphidius ervi*. Czechoslovakia.

dius ervi, was effective in early spring as a parasite of *Acyrthosiphon pisum* on alfalfa, in such a case the introduced parasite must be colonized at the period when the indigenous parasite action is lower (Fig. 316).

(d) Alternative hosts. The presence of an alternative host in the surroundings of a colonization site is rather useful for parasite establishment as it enables the parasite to survive eventual periods of absence or low density of its host (the pest). For example, the lack of an alternative host prevents the survival of *Aphidius smithi* in some areas of California (v. D. BOSCH et al. 1966, etc.). Thus alternative hosts must be kept in mind when the colonization site of an introduced parasite is selected. Host specificity features and factors influencing it should be considered. For example, because of the host range of parasites of many *Aphis* species and allied genera, we can expect that a parasite attacking several species of this type in its home will adapt itself to other similar hosts in the country of establishment, the specificity of indigenous parasites may show a certain relation of this type. We must look for such probable suitable alternative hosts, namely the economically indifferent species. It is an open problem in biological control to introduce economically indifferent (monophagous) aphid hosts into a country, with the aim of introduced parasite conservation. For example, *Longungius donax*, an aphid species restricted to a reed, *Arundo donax*, is an alternative host of *Aphidius transcaspicus*, which is a valuable parasite of *Hyalopictus pruni*, a cosmopolitan pest, in southern Europe, as far as to the Middle East, and C. Asia. The introduction of the indifferent aphid would not mean an economic loss due to its food restriction to reeds (weeds) and it would represent a source of alternative hosts for the beneficial parasite (see: foci, host specificity, etc.).

(e) Weather. Although generally favourable for some time, the weather conditions can quickly change and have an adverse effect on the colonized parasite population (heavy rain, wind, etc.). The colonization site should have a maximum protective cover for the parasite (see v. D. BOSCH & TILFORD 1964).

(f) Pesticides. Treatments with non-selective insecticides can eliminate the introduced parasite population either directly or through the elimination of its host in a given plot. Such an adverse influence of treatment was experienced by V. D. BOSCH et al. (1959, etc.) when trying to control *Therioaphis trifolii*. We also ascertained a fatal influence of non-selective treatment to introduced populations of *Aphidius transcaspicus* in a peach orchard in Czechoslovakia. Because of this possibility, in a colonization site an insecticide treatment should be prevented either completely, or for a considerable period (see: V. D. BOSCH et al., 1959, BARNES 1960, V. D. BOSCH & TELFORD 1964, SHANDS et al. 1965). DEBACH & BARTLETT (1964) recommend a prior organization of the colonization experiment in cooperation with large agricultural organizations to prevent the treatment of the site; or to choose gardens or neglected or abandoned plantings.

(g) Cultural practices. Cultural practices, such as harvesting or ploughing, influence the stability of the stand considerably and perhaps basically. The colonization sites should be chosen in order to minimize such influences.

– Timing – Timing of parasite release should be planned with respect to the season and day-time.

The period of the most favourable host occurrence and weather conditions should be selected. These two conditions need not occur simultaneously, as weather favourable for the host need not be suitable to the parasite introduction. Moreover, during a certain period of host occurrence the indigenous natural enemies may be rather effective, so that it is better to release the new parasites at a moment when this factor is less significant. For example, it seems that the release of *Aphidius smithi* in early spring in Czechoslovakia failed because the early spring weather, when the aphid population begins to develop, seems to be too cold to the introduced species, and the native parasite is highly effective just during this period; however, later in the season, the native parasite is not able to limit the increasing aphid population and the weather is warmer. Seasonal occurrence of the host should be known, so as to avoid the release at times of its population decrease. Character of the stand (annual and perennial crops, etc.) and host migration should also be considered.

As shown by DEBACH & BARTLETT (1964) the day-time under generally favourable weather conditions can be of importance. Releases in the morning, when the parasites usually emerge and mate, reserve the parasite the warm day hours for oviposition, orientation and for seeking protected microhabitats. Release in brilliant sunlight is known to stimulate rapid dispersal of some species of entomophagous insects. According to CLAUSEN (1951) release in the evening at dusk restricts dispersal while still allowing time for orientation to the new surroundings; this might be a desirable method during the warmer part of the year (DEBACH & BARTLETT).

We have mostly released the aphidius during the morning hours, but the above mentioned viewpoints should be also taken into consideration.

– Origin of colonized material – The colonized material may principally be from the two sources:

The release of material that was reared in the laboratory is the most generally followed method of parasite colonization. A certain release number of parasites is transported from the laboratory rearings and colonized at a given site. This method has an advantage in that the exact number of the released material is known. It must be applied at the initial stage of parasite establishment when no field collected material is obtainable in the area. Under certain circumstances, for example, if the host aphid is reared with difficulties or the receiver was not able to rear enough satisfactory laboratory stock of the host, we release the original shipped material; however, even then the introduced material must be reared first in the quarantine

laboratory and only then the emerged parasite adults are used for release—thus, we principally use the laboratory stock as well. We also undertook a direct release of imported material of *Aphidius transcaspicus* in Czechoslovakia: there was insufficient knowledge of its biology at the time of introduction, its propagation on *Aphis craccivora* as unnatural host was unknown and the host aphid *Hyalopterus pruni* was occurring only on Prunus trees in spring; in our experimental greenhouse we had only the secondary host plant, *Phragmites communis*, the common reed. Later in the season we transferred both aphids and parasites as the laboratory stock to the laboratory rearings from the release site in nature.

It is a common praxis to translocate the parts of plants attacked by aphids that are mummified by an introduced parasite to other sites to release the parasite there. This partially saves the production of mass-rearings. However, if we wish to follow this method, the parasite must be successfully established in a certain release site from which samples of material are then taken. This method was used by V. D. BOSCH et al. (1959), BARNES (1960), when transferring alfalfa plants with mummified aphids from one field to another. We have also followed this method when translocating the plum tree branches with mummified *Hyalopterus pruni* in *Aphidius transcaspicus* introduction experiments in Czechoslovakia, V. D. BOSCH et al. (1959) (see: methods) developed a special large-scale collection method using a specially constructed mechanical collector.

— Storage of material — Mass-rearings often give their production during a certain time before the required release number is reached. However, the longevity of parasites, even if fed on honey, is relatively short under optimum temperatures occurring in the rearings. For this reason, the adult parasites are kept separately under lower temperatures. The level of temperature must be experimentally tested. For example, WIACKOWSKI (1960) recognized that more than two weeks at $+10^{\circ}\text{C}$ temperature had an unfavourable effect on the reproductive capacity of *Aphidius smithi*. Storage at $+14^{\circ}\text{C}$ seems to be generally suitable, while lower temperatures must be dealt with experimentally.

We have found it useful to keep the stored parasites inside plastic bottles closed with nylon texture, in which wood wool or a piece of texture as a resting site for the adults were added: a few drops of honey served them as food. These bottles were later removed from the refrigerator ($+14^{\circ}\text{C}$), transferred to plastic ice boxes and transported to the release site.

In case it is necessary to accumulate the stored material or to store it for a longer time, it is recommended to move the containers with the insects two or three times a week from the low temperatures to about $+21^{\circ}\text{C}$ for 20–30 minutes (plus light). During this time the insects become active, feed and defecate. During this procedure it is always important to provide a supply of food and water. Otherwise, loss of vigour and increased mortality may follow. Honey seems to meet both requirements (See: FISHER & FINNEY 1964).

— Transport to the field — Temperature and R.H. conditions can adversely influence the transported material. This is generally known in the praxis of biological control, although different species manifest a different ability to survive the same conditions. For example, SCHLINGER & HALL (1960) observed when transporting samples of parasites in California, that some cool climate species such as *Aphidius ribis* died from the heat during transport while hot climate species survived it well. For this reason, the transported material must be given a certain protection from such adverse influences. DEBACH & BARTLETT (1964) mentioned that natural enemy containers, enclosed in a waterproof plastic bag or metal box, are kept cold by cloth gauze wrappings which provide evaporative cooling when moistened; or ice boxes and



Fig. 317. Opened box containing plastic bottles with living parasite material.

even refrigerated automobiles were used for transport of imported natural enemies to the release point.

We found that the transport of adult parasites inside plastic bottles, placed inside a plastic ice box was rather suitable. Some drops of honey and a piece of wet cotton wool were placed on the nylon texture that served as a part of the stopper of every bottle (Fig. 317).

Mummified aphids can be handled less carefully. We put the pieces of plants with the mummified aphids inside nyloncovered cages. It is recommended to place some wood wool among the pieces of plants to prevent possible injury to the mummies during transport. These nylon covered cages can be transported freely or inside the plastic ice boxes (Fig. 317).

Artificial foci units are transported in a closed car, covered with a large piece of nylon texture.

— Kinds of release — Inundative release is defined as a kind of release when an entomophagous insect is released to control a pest immediately, not through the action of its progeny (FLANDERS 1930, 1951). This type of control is mentioned to be similar to that obtained by use of chemicals since the mortality of the pest is more or less immediate and there is no prolonged interaction of the population. The method is probably best suited to univoltine pest species or multivoltine species which are injurious only during a single generation a year (DEBACH & HAGEN 1964). This type of release was not used in the aphidiids and, because of the multivoltine occurrence and long-termed injury of the aphids, it does not seem to be a perspective.

Inoculation release is characterized by the accumulative control action by the natural enemy progeny produced over several generations following the release of a relatively small number of natural enemies as compared to the host (DEBACH & SCHLINGER, 1964). It has been widely used in the biological control of aphids by parasites.

A

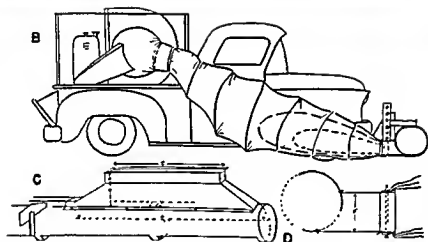


Fig. 318. Mechanical collector developed for large-scale field collection of imported parasites of *Therioaphis trifolii*. (A) collector in operation, (B) diagrammatic side view of collector - broken line invaginations in air duct indicate positions of collecting sacks; (C) diagram of one side of 'scoop' showing the adaptive collar with which it is connected to air duct; (D) lateral view of 'scoop' - note anterior opening (broken line) for entry of insect material and posterior opening through which material is drawn via adaptive collar into collecting sacks in air duct (V.D. BOSCH et al., 1959).

- Release methods - 1 Open release (a) Laboratory mass-reared material. The material transported inside containers from the laboratory mass-rearings is transferred to the chosen release site, where the containers are opened and the insects are either shaken out on the plants or the containers are left open to allow the adult parasites to disperse. This method has been commonly used by various workers.

(b) Artificial foci units (AFU). The units prepared in the laboratory are situated at the release sites. Although each unit includes a layer of soil in which the plants grow, it is useful to sink them partially into the soil to minimize the dessication of the soil

inside the units which would weaken the plants; if this is done, the units may be in function for a longer time.

(c) Mummified aphids. When the introduced parasite has become established in a certain plot and reached a relatively high density, we transfer the infested plants or their parts to other release sites. This method was used, e.g., by V. D. BOSCH *et al.* (1959), BARNES (1960), who transferred cut alfalfa plants with mummified *Therioaphis trifolii*. Similarly, we have transferred small branches of plum trees with mummified *Hyalepterus pruni* from one orchard to another. This method can be utilized when the mummified aphids on the plants are numerous enough.

(d) Field mass-collected material. When the introduced parasite populations become sufficiently high in relatively large plots, they can be collected for the purpose of releasing them in other sites. Special mechanical mass-collecting methods have been developed (DIETRICK, SCHLINGER & V. D. BOSCH 1959, V. D. BOSCH *et al.* 1959, STERN, DIETRICK & MUELLER 1965) (Fig. 318).

It seems that these methods can be used only on homogeneous field crops while there will be obviously great difficulties in applying the method for instance in orchards.

2. Semi-confined release. Practically, every confined release method is a semi-confined one, as after a certain period the confined populations are left to spread freely in the neighbourhood. We have, however, developed a method which is an intermediate stage in that the introduced populations are semi-confined from the date of release. The method is relatively simple: on branches of trees or on a release plot we place a nylon sack or nylon-covered cage, but leave the sack partially untied or the cage partially open. This allows the emerged parasites, when searching for hosts, to spread from the release cover, while a certain part of the population remains inside the cover. We have used this method successfully in *Hyalepterus pruni* control program in Czechoslovakia, where the released *Aphidius transcaasicus* occurred both inside the sacks (cf. confined release, fig. 319) and in the close environs; their spread was easily ascertained because the mummified aphids are brown-yellowish and differ from the mummies of the indigenous parasites. This method requires a relatively high infestation of the release plot by the host aphid to enable the parasites to find their host quickly in order not to spread too far and keep a relatively dense population at the release plot.

3. Confined release. (a) Nylon sacks on branches of trees. We select a small or large branch of a tree which is heavily infested with the host aphid, put the nylon sack over this branch, introduce there a certain number of parasites and we tie the sack with a rope. If the original aphid population is low, we add other aphid infested leaves or branches to increase the host density inside the sack, as far as possible, all the predators and mummies of indigenous parasites are removed. If the branch is strong enough, the simple tying will do, while on thinner branches or if we had used a larger sack, we tie the sack to several other branches in addition (Fig. 319).

(b) Metallic constructions covered by nylon texture. Constructions of various dimensions covered by nylon texture are situated at certain plots over the plant cover. The constructions, because of eventual wind, must be well fixed to the ground. Either the present aphid populations can be used, or we can add more aphids into the cage. When the parasite density inside the cage is high enough, as may be recognized from the number of mummies on the plants, the cages are removed and the parasites are allowed to spread to the surroundings. V. D. BOSCH *et al.* (1959), when using the caged populations in release of *Therioaphis trifolii* parasites in California, after the release of a certain number of parasites into the cages, introduced periodically stocks of aphids to further enhance the parasites and



Fig. 319. Colonization of parasites. Nylon texture bags situated on the parts of a tree which are infested by the pest aphid controlled.

to maintain a constantly high infestation level within the confined area. During the period of this colonization from April through to June 1956, releases were made at approximately weekly intervals with 14,400 *Praon exoletum* and 5,860 *Trioxys complanatus* being introduced into the experimental large organic cage. After a certain period aphid mummies produced by the parasites were abundant and the cage was opened to permit the spread of the adult parasites from the focus. Simultaneously, the staggered cutting cycle of the alfalfa in the surrounding area was introduced to make the aphids continuously available to the parasites. Under these conditions the parasites spread very rapidly, quickly established themselves throughout the 5-acre experimental area, and then moved into the commercial alfalfa adjoining this area.

(c) Polyethylene covers. This original method of ours was experimentally used during the introduction experiments with *Aphidius smithi* in Czechoslovakia. Polyethylene continuous row covers are commonly used in horticulture. Their primary role is frost protection. SHADBOLT (1960) stated that the shape, size and the perforations or ventilation of the covers greatly influence the heat-build-up in the soil during the day. A number of various other authors in horticulture have dealt with the microclimate of these protected or covered grounds (KOLJAEVA et al., 1966, see: greenhouses). We have preliminarily used these covers, although in a somewhat different manner. We built large tents constructed from polyethylene covers, each being $0.60 \times 2 \times 12$ m in dimensions. The borders of the tent were pressed close to the ground by a fixed rope and pegs and slightly covered with soil. There were 3-4 windows cut in the cover, about 30×30 cm, covered by a nylon texture to allow air-exchange during possible overheating at mid-day hours on sunny days, but preventing the parasites from spreading to the surroundings as well as the invasion of other elements from the outside. These tents were constructed on an alfalfa field in early spring, at the period when *Acyrtosiphon pisum* began to hatch from the over-

wintering eggs. After the plants have somewhat grown due to a higher temperature inside the covers, the experiments began, the aim being to recognize the influence of such a manipulation of the environment on the seasonal occurrence of the inside fauna, and, secondly, to recognize the survival of *Aphidius smithi* in such an environment, while the cold weather in early spring is unfavourable even to the native parasites. In one of the tents, the original population of the aphid was left untouched, while a number of laboratory aphids were added to another tent to provide for the introduced *Aphidius smithi* enough suitable hosts, as the fundatrices of the aphid are relatively scarce in spring. Although the general preliminary investigations seem to show that the introduced parasite failed to establish in such an early yearly period, we observed that the indigenous parasites, which could not be separated from the caged populations, as well as the aphid hosts, developed about twice as rapidly as the free populations in the surroundings. These experiments should be carried out on a larger scale. The continuous tunnel covers might be useful and cheap for this purpose. It is possible that the principle of the method could be useful even in the augmentation of the indigenous parasite occurrence and they could limit their hosts in a rather unnatural way. The covers could be situated as strips, etc. Similarly, the covers could be useful in the establishment of other introduced parasites of pest aphids on some other crops.

4. Comparison. Generally, with respect to the possibility of their application the release methods can be divided into two groups:

The first group may be applied when the first releases are made. It includes the great part of open release methods, and semi-confined and confined release methods. The release of laboratory reared material is rather easy, but the released parasites may spread too far and the populations fail to establish: this was recognized by V. D. BOSCH et al. (1959) during the initial stages of *Therioaphis trifolii* biological control program in California. However, we know other cases (Hawaii, see: release numbers), when a relatively low release number was sufficient for parasite establishment. An artificial foci unit method seems to be favourable in allowing the alternative, unnatural or even the pest host to be used in the program, temporary foci of parasites in the new environment being created; however, a greater number of AFUs are connected with certain difficulties as to their transport (weight, dimensions). All the open release methods have an advantage in that no further care is necessary for the released material. Semi-confined release seems to be useful both in concentrating the introduced population and allowing the simultaneous spread, further care being unnecessary. Confined release methods require at least periodical care in adding the new parasite material, checking the parasite density inside the cages, or in the final removal of the cage. A disadvantage of all the confined release methods is that the cages or sacks are easily visible and they can be damaged by uninformed people.

The second group includes the methods used only after the parasites have become established. They are useless during the initial stages of parasite establishment. Translocation of pieces of plants on a mass scale is usually a time consuming and expensive process (see: V. D. BOSCH et al. 1959), while field mass-collection of introduced parasites for further mass-release needs special mechanical equipment. However, just the use of these methods was rather useful in spreading the introduced parasites of *Therioaphis trifolii* in California on a wide scale.

There is no doubt that open release does not prevent the introduced parasite populations from the action of other members of the aphid-natural enemy food chain. The predators or fungi can cause the decrease of introduced parasite populations (see: V. D. BOSCH et al. 1959) for example, if the release numbers are relatively

low, mass-release of field collected material is useful in diminishing this influence because of the high number of individuals, but it cannot be used in the early stages of an introduction program. The confined release protects the introduced parasite better from eventual competitive relations in the new environment at the time when its density is relatively low.

— Release material — In general, we can release all the developmental stages of parasites, but each stage has certain negative and/or positive features.

Living parasitized aphids, if released in large quantities, can serve as an artificial temporary focus of the parasites as they feed on plants in the release site and are later mummified by the parasites which then emerge at the very same plot. Our method of Artificial Foci Units (AFU) is a practical example of the use of living parasitized aphids. The release of parasitized aphids is useful if specimens of an alternative host are released, otherwise it would mean a partial release of the pest population. Even the latter case is known to be advantageous in release experiments performed with other parasite groups. Nevertheless, in no case may the pest population that was accidentally brought from abroad with the shipped parasite be released even if it were via parasitized aphids: on the one hand, even the laboratory population is never completely parasitized and a certain number of aphids escape parasitization, on the other hand, even parasitized aphids may be able to produce a certain number of unparasitized progeny.

Mummified aphids, containing last instar larvae or parasite pupae represent another kind of release material. They are useful because of easy transport, but their main disadvantage is that they are unable to change their position in the case of adverse atmospheric conditions, as mentioned by WIACKOWSKI (1962). Moreover, the parasites mostly do not emerge simultaneously from the mummies, the emerging parasites disperse in search for mates and hosts, so that the initial released population becomes relatively less dense; the less probability of mating seems to be the main disadvantage; a great number of mummified aphids would be necessary to compensate this.

The adult parasites seem to be the best material for release if their release is well timed with respect to weather conditions and host occurrence. The adults collected in mass-rearings usually mate so that mated ♀♀ are practically released as a result and the initial establishment is more probable. The adults are also able to find suitable shelters and microclimate. The disadvantage of adult parasite release is that the adults disperse to the neighbourhood and the initial population becomes less dense; this can be compensated by suitable timing and release methods.

We can release either one species or several species simultaneously in each release site. There were some opinions in the past that each species has to be released separately to prevent competition. However, as shown correctly by BARNES (1960) who also began the experiments on *Therioaphis trifoli* parasite release in Arizona by releasing only a single species in a release site, several species, when released simultaneously, spread and become effective according to their specific features: *Praon exoletum* and *Trioxys complanatus* were established in Arizona when liberated simultaneously, but the latter species became more important because of its preference for a hot and dry climate which is just typical of Arizona. Similar results were obtained earlier by V. D. BOSCH (1959). Naturally, the mentioned case must be applied to other species with respect to their original habitat requirements: forest species should be released in forest type habitats and steppe species should be released in steppe habitats, etc. (see: host specificity chapter).

— Release numbers — 1. Underpopulation problems It is well known that in natural populations the reduction in the value of innate capacity for increase associated with

increasing sparseness of the population may be carried so far that it becomes negative and the population proceeds to dwindle to extinction. There are two aspects to this phenomenon: one is the final extinction of a population which has been well established in an area which has been brought down to low numbers by natural vicissitudes or deliberate destructiveness of man. The other is the failure of a small colony of immigrants to become established in a new area which is favourable in all respects except for sparseness of the colonizing population (ANDREWARTHA & BIRCH 1954). It is just the task of biological control praxis to determine the density of the introduced population to prevent its underpopulation and extinction. Naturally, this is not easy and we try to concentrate the released material at a single site up to a certain limit.

2. Acreage of crop. STERN & V. D. BOSCH (1959) commenced one of their papers on biological control of *Therioaphis trifolii* in California as follows: "When the spotted alfalfa aphid *Therioaphis maculata*, appeared in California in 1954, the state was faced with a serious agricultural problem, for this insect threatened the very existence of the great alfalfa industry. Alfalfa is a basic agricultural crop in California, with an annual planting of well over a million acres . . .". The less informed people are in doubt whether the relatively few introduced parasites can succeed in controlling the pest. In such a case we must not forget that also the pest was initially rare, but favourable environmental conditions allowed it to reach outbreak numbers. If the introduced parasites succeed in establishing themselves successfully in such an area, they may play a considerable part in the environmental control of the pest. We have at least two examples: *Therioaphis trifolii* and *Acyrtosiphon pisum* and the role of the introduced parasites in California.

3. Release numbers. As correctly mentioned by DEBACH & BARTLETT (1964), there is no means by which one could reliably estimate the minimum number of any natural enemy which must be released in order to procure establishment. For example, according to V. D. BOSCH et al. (1959), great difficulty was encountered with open-field colonization of parasites of *Therioaphis trifolii* in California in 1955; somewhat better results were obtained by concentration of release material under field cages the following year; however, permanent colonization at all release sites was almost constantly successful after millions of the specimens were available for distribution from established colonies. BARNES (1960), who colonized the parasites of the mentioned aphids in Arizona, gives a number per single site from 250 to more than 56,000. On the other hand, relatively low release numbers were used when *Aphidius smithi* was introduced into Hawaii to control *Acyrtosiphon pisum* but today's results of the control are spectacular: total number released 3,605 specimens, i.e. Nov. 1960: 750, Jan. 1961: 655, Feb.: 200, March: 2,000 (Annual report, 1960-1). For comparison, colonization of the same parasite species undertaken in California was as follows (HAGEN & SCHLINGER, 1960): releases started in alfalfa fields in May 1958 and by May 1960 more than 220,000 parasites had been released, the parasite became established even in several locations where as few as 100 individuals were released at the same time. In another case, the size of each colonization of *Troxys pallidus* in California during the *Chromaphis juglandicola* biological control program ranged from less than 100 up to 1,200 parasites, a relatively small number being apparently satisfactory for preliminary establishment (SCHLINGER, HAGEN & V. D. BOSCH 1960).

- Continuation of release period - The continuation of a release period has been an object of long discussion. DEBACH & BARTLETT (1964) mentioned, as a very general rule, that excessive difficulty in the initial establishment of a species indicates a lack of adaptability to the new environment and the probability of subsequent ineffectiveness in providing complete control. CLAUSEN (1951) has suggested that on the basis

of practical experience most species that turn out to be highly efficient become established readily, given suitable release conditions, and indicate their potential ability to get the host under control within the period of three years following the initial release (see: recovery).

Although these statements, being based on many years' praxis and statistical analysis, are undoubtedly correct, we should like to add some remarks. First, in case of failure of (permanent) establishment, it is necessary to carefully revise all the possible causes of these difficulties that were recognized during the colonization program (release method, character of the stand, host and parasite biology peculiarities, etc.). This could last for more than three years. Further, an introduced parasite may be valuable also in exhibiting partial control—just an integrated control program considers the partially effective natural enemies to be useful.

Another point of view on parasite release is how often a parasite population has to be colonized during one year. For example, STUSS (1967) made colonization experiments in 1961 and 1962 in the late summer months only, while in 1963 the colonization began in May and was periodically continued until August. There is no doubt that periodical colonization at the same plot within one year can diminish the influence of possible adverse conditions (weather, host aphid life-cycle, action of other natural enemies, etc.), as these change during the season while a single colonization may just be influenced adversely and fail in consequence.

- *Recovery.* Sampling for recovery is undertaken about the interval when the first mummified aphids occur at the release site. This interval is approximately 10, 15 and 20 days, depending on the climatic zone and period of the year. The pest species, which should be attacked by the released parasite is dealt with first, and then we also collect samples of other aphid species to recognize the eventual adaptation of the introduced parasite to other aphids occurring at the release site or in the environs. If no mummies are found, we collect even the living aphid material and rear it later under laboratory conditions with the purpose of establishing the mummies.

- *Initial establishment.* - The successful sampling for recovery shows that the first generation of the released parasite survived in the new environment and we can thus consider the species to be initially established. Periodic samples are then taken throughout the year and the occurrence of the released parasite is studied. The evaluation of results shows some release sites to be unfavourable owing to climatic and weather conditions, while difficulties in establishment ascertained in a large or prevalent part of the release sites are a sign of a more serious matter, based on host life-cycle, different dispersal of the host and parasite, etc. As the season advances we take samples in wider surroundings of the original release site to establish the spread of the introduced population.

Recovery samples are taken with the qualitative intention of recognizing whether a parasite was initially established or not, or quantitative methods can be applied to recognize the effect of different release numbers in the first and following generations of the initially established population.

Initial establishment is a more or less simple matter. A number of introduced parasites become initially established in the country of introduction. The reason is obvious: in most cases, at least during the period of partial scientific approach to parasite introduction, the introduced parasites are released in a suitable period of the year and in the presence of a host.

Records obtained during the initial establishment process give us the data from the first recovery up to a period of less than one year later.

The reared material from the recovery samples should be preserved for taxonomic purposes.

- Permanent establishment - Under permanent establishment we understand the establishment of a parasite for more than one year from the date of initial release. One year is just the period in which the influence of seasonal peculiarities on the introduced parasite may become obvious, at least partially. It is well known that in the course of a year there are several periods which could be critical for the establishment: these need not be only climatical, but include peculiarities in the host life-cycle, etc.

Although one year reveals some information, several successive years are necessary to recognize the true ability of a parasite to survive and occur in a given country. One extraordinary year may be fatal for the established parasite population, which is able to survive only average years. During permanent establishment research, we can also recognize the effectiveness of the parasite with respect to the controlled pest as well as to its occurrence and spread in various districts of the country of establishment. This can be illustrated by the results of the *Therioaphis trifolii* parasite introduction program into Arizona, U.S.A. (BARNES 1960): *Praon exoletum* was released at 13 sites and recovered at 8 of them between October 1956 and September 1957. The number released at one site ranged from 400 to 26,000. Recoveries were made at or near some of the release sites and in all months. In 1957 parasitization was low, the highest observed was 1.1% in a plot where 2,200 adults were released and 6,000 pupae. In 1958 the parasite was recovered at only one location. Recoveries were more numerous and widespread in 1959. It appeared (1959) that the parasite established itself in south-central Arizona and spread considerably northward but did not increase sufficiently to be of economic importance in the pest control. Another parasite, *Trioxys complanatus*, was released in numbers of 384 to 4,725 between November 9th, 1955 and June 7th, 1957 at 13 sites. In 1957 it was recovered at 3 sites, widely scattered over the release areas. Parasitized aphids were found most frequently in a release plot where 4,725 total adults were liberated. The parasite spread between July and September considerably, but was of little economic importance, the indication of highest parasitization at one release plot being 3.28 to 12.2%. In 1958 the parasite spread rapidly and widely. There was 5 - 10%, 1 - 20%, 40 - 90% parasitization ascertained in various fields, the average being 14.6%; the parasite evidently was of economic value in reducing the pest populations in central Arizona in 1958. By the end of 1958 the parasite was clearly well established in the principal alfalfa growing areas across the southern third of Arizona. Samplings in 1959 showed the further spread and abundance of the parasite; the average parasitization in February was 38%, but declined rapidly early in spring and remained low for the rest of the year, being only 0.16% in October. In 1960 parasitization was very low (4.9, 7.4, 13.6% in February). Permanent establishment in Arizona of both parasites manifests the same features as to the local climates as in California: the parasites were distributed in accordance with their requirements, so that *Trioxys complanatus* found the hot and dry climate of Arizona favourable, while *Praon exoletum* preferred cooler and more humid areas.

Permanent establishment is a rather important phase in the colonization program. As mentioned by DEBACH & BARTLETT (1964), in the colonization of a new importation the primary objective is to obtain permanent establishment in at least one locality which may be used as a focal point for natural spread or as a source for further manipulated distribution of the species. The significance of the possibility of taking mass-field samples became obvious during the *Therioaphis trifolii* parasite introduction program in California, where just the spread of the parasites was possible owing to the mass-sampling material in permanent establishment plots and its release in other sites (see: V. D. BOSCH et al. 1959, 1964).

Similarly as in an initial establishment period, a part of the samples collected

during permanent establishment recoveries should be preserved in collections.

– Spread – The research of parasite spread from the original release sites is a rather significant part of the recovery phase of the introduction program. Data on the gradual spread of the parasite assist us to recognize the acclimatization of the species in various areas with different local climates. General maps on parasite spread in the country of establishment are rather useful. They have been used in the research of the spread of introduced parasites of various pest aphids in California (*Therioaphis trifolii*, *Acyrtosiphon pisum*, *Chromaphis juglandicola*).

Spread of the introduced parasite may be natural (see: dispersal, spread) or the field-populations, collected at the sites of establishment, may be transferred to other release sites (see: V. D. BOSCH et al., 1959).

– Food chain – Permanent establishment of a parasite species in various release sites and results of the search for its occurrence in the surroundings of the sites are the source of records that enable us to classify the position of the introduced parasite in the food chain associated with the given pest aphid. It is well known that we may never introduce a parasite into the really same environment as that of its native country:

If we introduce a species to control the native pest in a country, there is a native community to which the pest belongs and there naturally occur some biotic agents that limit it to a certain degree. Thus, in this case, the parasite must find its place in the community. For example, this is the case of introduction of *Aphidius snuthi* into Czechoslovakia to control *Acyrtosiphon pisum* on alfalfa, where the native parasite, *Aphidius ervi*, plays a more or less significant role in aphid limitation during the season.

On the other hand, if we have an introduced pest and try to control it by transferring its original parasites from its home into the country of its establishment, even here the community is different with respect to parasites; it is well known that various crops are often world wide in distribution and their fauna consists of cosmopolitan pests plus indigenous elements. Thus, an introduced aphid pest will be partially attacked by the natural enemies that occur in the country of its establishment, and the introduced parasite must again find its place in these new and developing food chains. We can mention two examples: *Chromaphis juglandicola* is an introduced pest aphid on walnut in California. The indigenous Californian coccinellids play a significant role in its limitation. The introduced parasite, *Trioxys pallidus*, which had other conditions in its native country, must adapt itself to the new interspecific relations. Another example is *Therioaphis trifolii*, an introduced pest of alfalfa in California: native parasites were brought from the Old World to California but the aphid was attacked here by the native coccinellids, which caused some difficulties in the initial establishment of parasites, even when the parasites become successfully established, the coccinellids play a further rather significant role and the parasite must develop new interspecific relations, different from those in its home.

Interspecific relations with respect to other natural enemies are not the only relations of the parasites in the new environments. The parasites may find some other aphids that occur in the release sites or in the surroundings, to be useful as hosts and may include them into their host range. This is, for example, the case of *Trioxys pallidus* in California. The parasite attacks a number of dendrophilous callaphidid aphids in its home, but it was introduced into California to control *Chromaphis juglandicola*. None of its other native hosts occurred in California, so that the parasite was restricted to a single host, *Clir juglandicola*, by this transfer. Nevertheless, it found a native callaphidid species, *Tinocallis caryaefoliae* and successfully parasitized it (see: SCHLINGER, HAGEN & V. D. BOSCH 1960).

- Failures - World classification of the introduced natural enemies has shown that many natural enemies fail to become established, about 60 - 80% according to CLAUSEN (1956), or if established, fail to control the host because of some slight shortcoming in adaptability or because of disadvantage caused by adverse environment (DEBACH & HAGEN 1964). Thus, failures in establishment often occur. But a failure in parasite establishment does not always mean that a parasite is not capable of occurring in the country of introduction; there are a number of factors that can cause this failure and their action must be analyzed before any definite conclusion is made.

1. Climate. Failure to adapt to the new climate is responsible for more failures in colonization than any other factor (DEBACH & BARTLETT 1964). Climatic conditions may be very similar both in the country of origin and of introduction, but the weather of so-called climatic areas may differ considerably in different parts of the area during different seasons, and microclimates will vary even more. Average monthly or yearly temperatures and humidities tell us little about the differences between localities within similar climatic areas. The insects involved are affected more by the extremes of heat and cold than by the average temperature (assuming it to be suitable to begin with) (DEBACH 1962).

It is well known that climatic zones which are rather extreme in heat and cold, such as the temperate zone and hot arid districts of the subtropics, can be responsible for the failure in parasite establishment, although the parasite may be able to survive the milder periods of the year.

The significance of climatic conditions can be clearly documented by the establishment and distribution of introduced parasites of alfalfa aphids in California: of the parasites of *Therioaphis trifolii*, *Praon exoletum* was not capable of surviving in some areas of California where summer conditions are rather hot and dry. Similarly, the same conditions were highly unfavourable to *Aphidius smithi*, a parasite of *Acyrtosiphon pisum*.

2. Character of the stand. As mentioned earlier, the parasites are generally rather dependent on the type of habitat in their distribution and may not be capable of occurring in another kind of habitat although the host aphids occur in both kinds of habitats. The annual or perennial character of the community is also important with respect to parasite conservation.

3. Aphid host plant. Aphid host plant seems to be important in influencing the shape and often also the density of aphid colonies.

4. Physiological sustainability of the aphid. The physiological differences in separate stocks of the host aphid with respect to parasite action are rather difficult to establish.

5. Aphid life-cycle. It is well known that the aphid life-cycle exhibits certain modifications depending on the climatic zone. Quiescent states in aphid development and migration must be carefully examined as they can influence the coincidence of the host and parasite considerably.

6. Release numbers, release techniques, release period. Release numbers of parasites can be rather different in dependence on the life-cycle of aphids. In the case that the parasite must disperse to follow the aphid in the same or similar kind of habitat, its released population must be initially much higher than if they both occur at the same plot throughout the whole season. For example, in the dioecious aphid species, such as *Hyalopterus pruni* in Czechoslovakia, the initial released population of *Aphidius transcaasicus* must obviously be much higher than it was in our experiments: the aphids migrate from plum trees (orchards) to reeds, and, although the habitats may be rather close to each other or often mixed, the parasite is unable to spread very well when following the aphid as it prefers lower instar aphids to

parasitize, mass-release and mass-occurrence of the parasite on plum trees could increase this probability, while low parasite populations are unable to survive in plum orchards after the migration of aphids. Release date and release period could be responsible for parasite failure owing to unfavourable weather conditions.

7. Selection of unsuitable strain of parasite. Although the importation of material originally reared from the same host in its home is generally preferred, the introduced stock can be reared from another host, if the pest is attacked by the parasite in a part of its distribution area at least. However, there may be certain strains or races, which fail to establish as parasites of another host, the pest, in the country of introduction. For example, a stock of *Lysiphlebus testaceipes* from California would fail to control *Aphis spiraeicola* in Europe or in the Far East, as the parasite attacks the aphid in California but does not complete its development on it. On the contrary, stock of the parasite obtained from Cuba could be successful, as the parasitization of the aphid by this parasite in Cuba is common and the parasite development is complete.

8. Searching ability of the parasite. This is a rather important phenomenon. When the host becomes scarce, the parasite must be able to find it also at such low densities otherwise it will fail to survive during the period.

9. Lack of alternative hosts. A parasite is often introduced into a country where its alternative hosts do not occur. Consequently, the parasite is much more vulnerable through the seasonal lack or low density of its single host species, as it cannot find other hosts in the environments. For example, the lack of alternative hosts is known to cause failure in permanent establishment of *Aphidius smithi* in some districts of California, where the host aphid is temporarily absent because of unfavourable weather (see: V. D. BOSCHI et al., 1966).

10. Spread and dispersal. Spread and dispersal mean that a parasite population becomes rather scattered in another plot and fails to establish because of lack of mating, etc. Slowly dispersing species are less handicapped in this respect (DEBACII & BARTLETT 1964). Deuterotokous and thelytokous parasite populations are more useful here as they do not need to mate and their populations can establish although originally rather scattered. Naturally, the density of the spreading population and mode of spread are rather important.

Permanent establishment of a parasite depends also on the spread and establishment of the host. For example, as mentioned by DICKSON (1962), *Therioaphis trifolii* was introduced into North America in 1953, only parthenogenetic populations being known. Consequently, during the following years of its rapid spread and establishment to new areas it reached a northern limit over which it did not reproduce because it did not seem to produce viable eggs and consequently was not able to survive the winter period in such areas which were re-invaded each summer. It is obvious that the parasites were naturally not capable of establishing in such areas permanently either. However, a holocyclic strain of the aphid has later developed, which is identified by its ability to produce sexuales and overwintering eggs on alfalfa during the autumn. Because of this, the aphid is now present throughout the year in areas in which it was previously a late-season migrant or totally absent. We can therefore expect that the permanent establishment of the aphid will also soon be followed by the permanent establishment of at least some of its parasites.

11. Action of other natural enemies. Other natural enemies, especially predators and fungi, either indigenous or introduced, in an earlier period, could be responsible for failure in the establishment of introduced parasite populations, especially if the initial populations were relatively low. Higher release numbers are necessary or confined release methods must be applied to prevent the competitive action of other organisms.

12. Insecticides. Accidental and unexpected treatment by a non-selective insecticide can eliminate an established parasite simultaneously with the pest.

13. Agricultural practices. Some practices, such as harvesting, have an adverse influence on the parasite establishment, as they strongly influence both the microclimate of the stand and density of the host population.

Most of these factors do not take place individually, but in a complex with other factors, they often condition each other. It would be advantageous to follow a certain scheme and revise the separate parts of the program gradually in order to recognize the possible reason for failure in parasite population establishment.

— *Parasite effectiveness evaluation.* Evaluation of the relative effectiveness of natural enemies of the pest on a given crop or in a given ecosystem is a fundamental prerequisite to intelligent attempts to manipulate an insect population ecologically. Evaluation should be one of the first procedures, if not the very first, to be carried out in any new biological natural project. It furnishes a scientific ecological basis for applied biological control which otherwise would be largely empirical. Thus, if the potential capacities of all natural enemies on a given crop become known, the need for new importations or manipulations is evident. Evaluation should also point out or help the reasons why certain natural enemies fail to attain their potential (DEBACH & BARTLETT 1964).

— *Qualitative methods* — Qualitative methods of evaluation of introduced parasite effectiveness have both positive and negative features. Their extensive character allows us to cover a relatively great area in a short period, in general, we are able to recognize whether the parasite is established and whether it seems to be effective or not. Naturally, such an evaluation is a rather subjective matter, and it was correctly stressed by DEBACH & BARTLETT (1964) that much will depend on the wisdom, training and experience of the individual investigator. On the other hand, this is not an exact method and it could lead to misleading results as we cannot determine the role of separate factors which take part in influencing parasite effectiveness. According to our opinion, this method is useful when applied in early stages of a parasite introduction program, when the parasite starts to become a member of a community, or on the contrary, at the period of permanent and long establishment, when the effectiveness is generally known and well proved so that no new data are necessary.

— *Quantitative methods* — In the quantitative evaluation we use the same methods as when sampling populations of the indigenous parasites and establishing their effectiveness. These methods are dealt with in the chapter on natural limitation. Of these methods the stem-counting or leaf-counting seems to be the most useful, the percentage of parasitization being determined by dissection of the aphid material. In this connection, too, we should again stress the complex character of parasite effectiveness, as everywhere in this book. We can mention here the rather illustrative standpoint of SIMMONDS (1948): in order to gain some true idea of the value of a parasite species as a controlling agent it is necessary to study it in the field over a range of conditions, when its effectiveness is usually expressed far better in general terms than by a series of "percentages of parasitism", although the latter may be of use in conjunction with such a general description. DEBACH & BARTLETT (1964) strongly supported this standpoint, emphasizing that figures on per cent of parasitization used alone—as is often done—are of little value in predicting host population trends in the next generation; it can be shown by simple arithmetical models that in one case 98% parasitization will be sufficient to keep the host from increasing in the next generation, whereas with another species of parasite and host, 60% parasitization could result in a decrease. This merely serves to illustrate that a high degree of parasitization in itself does not indicate an effective parasite. Ideally,

population sampling should show long-term trends of actual mortality caused by the parasite, predator, or combination being studied. In order to do this, periodic samples must usually be taken over a period of several years and should take into account the number of generations of natural enemies to one of the hosts. Thus, a parasite population may have to be sampled several times during one host generation. The authors cited further correctly stress that many of the attempts to evaluate natural enemy effectiveness have been based upon periodic partial census of the host-natural enemy complex without taking into account mortality caused by other environmental factors.

- Analysis of ineffectiveness - An introduced parasite may be found ineffective, either due to the failure of establishment or it may become established but it operates below its potential effectiveness. Analysis of factors that could be responsible for such ineffectiveness must then be undertaken.

DEBACH & HAGEN (1964) summarized the factors in a rather useful review, as follows, abbreviation plus or minus with respect to the significance of separate factors in aphid parasites being added:

In the general habitat these factors include:

1. Adverse climatic factors such as heat, cold, low humidity, rain, wind (+).
2. Unfavourable host plants which fail to provide sufficient shelter or otherwise be unattractive (+; but the role of host plants is even more complicated).
3. Scarcity of water or of food for adult parasites owing to lack of pollen, honeydew or floral nectar (-; the parasites feed on honeydew, their adult food is present together with the host).
4. Severe competition with other species which may be constant or intermittent (+; predators, fungi, indigenous parasites).
5. Adverse effects of toxic chemicals applied to the crop or habitat (+).
6. Adverse effects of cultural practices (+).
- (7). We should also add lack of alternative hosts.

The host insect may be unfavourable or unsuitable:

1. Because of unsynchronized voltinism between the host and natural enemy or because of unsynchronized diapause (+; aphid migration should be added).
2. Because the host plant confers resistance on the host insect to the natural enemy (-).
3. Because the host insect represents a biological strain unsuitable to the natural enemy (+).
4. Because suitable stages of the host are periodically unavailable or scarce, so that enemy populations are decreased (+).

The entomophagous species itself:

1. ovarian diapause, migration, or aggregation away from the host population for a part of each year (+, but lack of coexistence with the host is due to peculiarities in the host life-cycle).
2. A low rate of reproduction either seasonally or constantly which, if further reduced by periodic environmental unfavourability, enables the host population to reach outbreak levels easily (+)
3. Disadvantages at low densities concerned with inability to find mates or with tendency to disperse (+).

There are different opinions of various authors on the definition of a parasite which is stated to be ineffective. CLAUSEN (1951) derived his three-generation, three year-theory from the analysis of world biological projects. according to this definition, an effective parasite or predator might be expected to reveal evidence of control at the point of release within a period of three host generations or three years. A

fully effective parasite or predator is believed to be easily and quickly established, while failure in establishment is an indication that it will not be fully effective after establishment is achieved. CLAUSEN gives several points with respect to which colonization may be discontinued after three years if there is still no evidence of establishment (colonization in each distinct climatic zone occupied by the host; colonies adequate in size and number; synchroization of releases; adequateness of recovery collection; biological factor directly affecting continued reproduction not involved). CLAUSEN's opinion was discussed by THOMPSON (1951), SELLERS (1953) and others. SELLERS believes that three years are not sufficient to recognize the effectiveness of an introduced natural enemy. In our opinion, three years are not enough to solve all the problems connected with the elucidation of the influence of factors mentioned by CLAUSEN, especially when the host and parasite biologies are poorly known. Further, CLAUSEN requires a full effectiveness of a natural enemy. In our opinion, first, a fully effective natural enemy seems to be rare, at least in natural enemies of aphids, but we meet a complex of natural enemies in nature; secondly, a fully effective natural enemy is a requirement of biological control, but with respect to integrated control just the partially effective natural enemies are important.

On the basis of analysis of the factors which could be responsible for parasite ineffectiveness, parasite augmentation and conservation may be dealt with.

- Augmentation - Periodic colonization. To enhance the population density of the parasite, periodic colonization should be undertaken. This method was found to be useful during a parasite initial establishment period (parasites of *Therioaphis trifolii* in California: see: V. D. BOSCH et al. 1959) in Arizona: BARNES 1960; parasite of *Chromaphis juglandicola* in California: SLUSS 1967).

Development of adapted strains. This seems to be a perspective method in aphid parasites.

Introduction of better adapted strains. Two strains of *Trioxys pallidus* were introduced into California. The stock from France was released, while another stock was later introduced from Iran which was probably better adapted to the conditions which occur in some warmer interior valleys of California (V. D. BOSCH et al. 1962). This seems also to be a matter of further research in aphid parasites.

- Conservation - Introduction of economically indifferent alternative hosts. Alternative hosts' presence is of fundamental significance. The alternative hosts (V. D. BOSCH & TELFORD 1964) damp oscillations in parasite and host densities, maintain functional parasite populations during low density periods of preferred hosts, provide suitable overwintering hosts, facilitate maximum parasite distribution, etc. In our opinion, as mentioned earlier and supported by an example, it could be useful even to introduce alternative hosts of the parasites, i.e. such species of aphids which are monophagous or rather restricted in their host plant range and attached to economically indifferent weed plants.

Hibernation sites. This means practically to protect the chronic foci of introduced parasites. There seem to be difficulties in protecting hibernation sites of parasites released on annual crops. SHANDS et al. (1965) when dealing with the introduction of *Aphidius matricariae* populations to control some potato aphids in Maine, U.S.A., in order to aid survival of the parasites during the first winter after release, cut many of the potato stalks in one field in the autumn and took them to the edge of the nearby woods so that autumn or spring ploughing in the field would not cover and destroy the parasites hibernating inside the aphid mummies.

ZONES. The perspective of biological control of various pests in separate climatic zones has been a subject of many discussions. Statistical records have shown that

most successes in biological control were reached in areas of warm or at least mild climates.

There is no doubt that the statistics are true. Nevertheless, with respect to the aphids, one should bear in mind that aphids are temperate-subtropical as to their origin and the greatest part of their species are found in these areas, while only a minor part occurs in the tropics, being either an indigenous or widely distributed (cosmopolitan) species. The distribution of their parasites, the aphidiids, is similar with respect to the zones. These features throw a different light on the biological control of aphids by parasites.

The following records are obtained when we separate the cases of practical biological control of aphids by parasites into separate climatic zones. Intentionally, we selected only cases where introduced parasites were used and the records are sufficiently satisfactory both as to the host and parasite, recovery records occur, etc. Abbreviations: establishment (+), no further records available or the work is in progress (?), no establishment (—).

Temperate zone. *Acyrtosiphon pisum*: USA, eastern states (+), Canada (?), Czechoslovakia (?), Poland (?). *Hyalopterus pruni*: Czechoslovakia (?). *Megoura viciae*: Czechoslovakia (—; field experiments not satisfactory). *Myzus persicae*: USA-Maine (?).

Subtropics. *Acyrtosiphon pisum*: USA, western states and California (+). *Aphis gossypii*: USA, California (?). *Aphis spiraeicola*: USA, California (?). *Brevicoryne brassicae*: Australia (+). *Cavanella aegopodi*: Australia (? +). *Chromaphis juglandicola*: USA, California (+). *Therioaphis trifolii*: USA, California (+), USA, western states (+), Mexico (+). *Toxoptera aurantii*: USA, California (+). *Tuberculoides annulatus*: Tasmania (+).

Tropics. *Acyrtosiphon pisum*: Hawaii (+). *Aphis nerii*: Hawaii (?). Various aphids: Hawaii (?).

These records seem to show that biological control work has been undertaken in more or less the same way in all the zones. However, the projects of Californian workers have been elaborated best, on a very broad basis, while a number of other records did not bring more precise results; there seems also to be a disproportion between the team work and work of individuals because of the state of research. These factors, perhaps, seem also to have an influence on the prevalence of success in the subtropics and tropics. However, if we deal with the objects of control in California, in detail, it is obvious that all the pests controlled are introduced species, occurring in stable stands and such features naturally influence the probability of the success of biological control in a positive way.

In general, the number of successes in biological control of pest aphids as control objects seems to be low for any generalization with respect to zones. We may perhaps classify the situation in such a way that while biological control work of aphids has become well organized in some subtropical and tropical countries, its development in temperate zone is at a more or less initial stage. There is no doubt that each separate zone has its own peculiarities, which may be both useful or adverse with respect to biological control of aphids by parasites.

As an addition, we should have perhaps to emphasize that biological control is classified in accordance with a certain degree of success; nevertheless, also partial control has been considered useful in the recent trend of integrated control. This criterion should stimulate biological control activities.

— ARID ZONE. The arid zone covers areas in all the climatic belts of the world. However, besides uncultivable areas such as the stone deserts, it includes a number of areas which have suitable soils, but the aridity makes them unsuitable for cultivation.

The climate of the arid zone of the U.S.S.R. is temperate, of a strongly continental character. Winters are severe, summer periods hot and dry.

If we summarize the situation in the arid zone of the U.S.S.R., it is obvious that there are two groups of aphid pests, which attack the grown crops: on the one hand, there are species which are the common and widely distributed pests associated with the crop, which have become distributed by following the crop cultivation in the arid zone, their distribution from other districts was gradual and they were followed by more or less complete complexes of indigenous natural enemies. On the other hand, there are native species associated originally with the virgin communities, but which have become adapted to the crop environments. There is the big problem of reservoirs of the aphid pests outside the cultivated crop fields and seasonal dispersal of the aphids to the crops. The climate is temperate.

- U.S.A. The greatest attention has been paid to arid zone problems in California and Arizona (BARNES 1960, V. D. BOSCH et al., various papers, DICKSON & LAIRD 1959, REYNOLDS & ANDERSON 1955, SMITH 1959, and other papers dealing with biological control in California and Arizona).

Problems of the arid zone connected with irrigation in California were summarized by SMITH (1959). Insects are classified to represent serious problems in irrigated lands. However, native insect species that have become major problems in irrigated regions in California's irrigated crops are introduced species (*Therioaphis trifolii*). Irrigation enables the rapid spread of the introduced pests because the physical environment is suitable and the food supply is almost unlimited during the major part of the year. The situation as to insect pests and irrigated lands in California is summarized in that there will be more insect problems with the development of irrigated agriculture, but the reasons for this are not primarily the result of irrigation development or practices, the reasons lie with the introduction of insects without their natural enemies, large monocultures, and the elimination of weeds that serve as shelter and reservoir of natural enemies.

The climate of California is subtropical, with very different microclimates in various districts. The winter period is mild, while the summers are hot.

If we summarize the situation in the arid zone of the U.S.A. (California, Arizona), it is obvious that most of the pests are introduced species, which have become widely distributed over the irrigated lands because of this suitable environment.

- Problems. Biological control problems in an arid zone become obvious from the main peculiarities of this zone: first, the occurrence of indigenous communities, second, cultivation of virgin lands and the development of new ecosystems associated with crop growing in climatically arid districts.

The development of the new ecosystems is rather important. As already shown, the irrigated lands represent rather favourable environments for certain species and increase of their populations: species of the indigenous fauna occur there and new immigrants appear in such areas, either due to gradual spread from other areas of crop growing or due to accidental introduction by man. In every case, the irrigated land environment decreases the influence of adverse climatic conditions as can be seen from the development of plant communities of a virgin and cultivated character: at the period, when the virgin communities become burnt by the sun during the hot summer, the irrigated crops favourably survive.

From the biological control point of view, it is rather important whether an aphid species occurs practically only in cultivated lands, or whether it is also associated both with the virgin and cultivated lands. The origin of the pest is also important because of the presence or lack of associated natural enemies. When a pest aphid is an introduced species and depends on the cultivated crops as to its occurrence, its control

to be less difficult as the natural enemies can be introduced and the pest can be under their control for at least a great part of the year. This is, e.g., *Therioaphis* in California. It seems, however, that in a greater part of the arid zone there are pests, either indigenous or introduced, which are connected both with the virgin communities and cultivated lands. This situation is more difficult as the reservoirs of pests occur continuously in the area and the pest disperses seasonally from there to attack the crop; annual crops are an especially hard problem from this respect. For example, e.g., the problem of *Aphis craccivora* on cotton (C. Asia). In this case, the pest should be controlled both in virgin and cultivated communities (see: multi-host control). This control could be at least partially reached by conservation of the indigenous or introduced parasites at the places where the sources of the pest are.

Alternative hosts of parasites seem to play a significant role in enabling the multiplication of parasites to occur continuously at such places. For example, in Soviet Asia, *Salix* trees are commonly attacked by *Aphis farinosa*, which is a holocyclic perennial aphid. This aphid is one of the common hosts of *Lysiphlebus ambiguus*, whose host range covers a number of various other aphids, including *Aphis craccivora*. We could expect that mixed shrub communities, where both *Salix* and *Robinia* locusts occur being associated with *Aphis farinosa* and *A. craccivora* respectively, could also mean that the parasites attacking both the hosts, should limit the population of *Aphis craccivora* that emigrate from *Robinia* stands to cotton fields. We could expect the parasites also to disperse to cotton fields, as, however, their dispersal is slow when compared with the pest aphid, integration of control could then be slow. Further research is necessary in this respect, but it is obvious that purposeful manipulation of the environment in accordance with parasite action could be useful. Another problem is the selection and introduction of parasites to be established in irrigated land environments. We have already mentioned that the physical environment of irrigated land differs from that of virgin lands. Consequently, we can expect that there might occur successfully also the introduced species unable to survive in virgin lands. This scope gives a wide field in parasite introduction possibilities. The composition of pest aphid fauna of crops grown in irrigated lands, where a number of widely distributed pests are found, shows the obvious perspective of biological control of aphids by parasites in the arid zone.

ISLANDS. In the earlier periods of biological control history, islands were supposed to be the areas where biological control could be possible and successful, while some attempts were thrown on the biological control in continental areas. If certain successes were reached in certain parts of a continent, such districts were classified as "ecological-islands" (IMMS, 1931. see: DEBACH & SCHLINGER, 1964).

These opinions, which had apparently been caused by the unequal level of biological control in islands and continents, were later deeply criticized and analyzed. One of these authors, THOMPSON (1928), may be mentioned, who has clearly shown the relative position of continent-island biological control relative value. He carefully analysed the problematics of biological control in continental areas and showed that the parasites of insects inhabiting continental areas play a real part in the natural regulation of their hosts. The increase and spread of the hosts-pests appears when they are transported to new areas where they escape from the action of natural enemies which are not replaced by any effective species in the new environments. The absence of natural enemies in the new environment seems to be the cause of the increase of the imported species and this is the reason for importing parasites in continental areas (DEBACH & SCHLINGER, 1964).

THOMPSON raised three objections as to the use of biological control in continental areas:

1. Comparison of the continents of Europe and N. America. There is a similarity between the biota of the two continents. The indigenous insect faunas of both these continents have in common many of the principal genera of injurious insects, and what is true of these pests is also true of their parasites.

2. The transfer of phytophagous insects from the Palearctic to the Nearctic region and vice versa should not produce any marked change in their economic status, in so far as this is regulated by their natural enemies, since there exists in both regions a variety of similar parasite species of polyphagous but of similar habit, apparently sufficient to replace automatically those by which the introduced insect was controlled in its native country.

3. Behaviour of hyperparasites. If a primary parasite is introduced into a new country, great care being taken to prevent escape of the secondary forms, the primary parasite is attacked in the new environment practically to the same extent by an almost equal great variety of hyperparasites.

The possibilities of successful biological control seem therefore to be equal both in the continental areas and in islands, although the relatively higher proportions of successful control has been obtained in islands (after DEBACH & SCHLINGER, 1964).

Although THOMPSON's conclusions are generally true for the aphid-parasite group as well, in our opinion it is necessary to note the following: there is no doubt that Europe and Nearctic America have a number of common features. Nevertheless, the similarity is the greatest in the northern parts, being gradually less, while the diversity is greater southwards, (see Geographic distribution, STARÝ, 1967). Naturally, there occurs a similar floristic zonation as in Europe. Nevertheless, according to the results obtained in connection with the research of different faunistic complexes of parasites in the Palearctic and Nearctic regions, there are no close relations between these continents except for the northern parts (forest tundra zone); certain connections of a closer character occurred apparently in much earlier times of geological history.

With respect to the relations of the members of separate faunistic complexes to an introduced aphid species, such newly introduced species is usually attacked by the members of indigenous faunistic complexes, while exceptions may be found in cases of very strictly taxonomically-ecologically separated species (details, STARÝ, 1967).

— BIOLOGICAL CONTROL. According to our studies based on the comparison of aphid and parasite fauna of separate islands, the basic and most important features with respect to biological control is the type of island, the kind of climate being also rather important. Although there are no strict differences between the continental and oceanic islands, the criteria used being true to a various degree in various groups, such classification of islands has been found to be acceptable for the biological control of aphids by parasites.

The aphid parasite fauna of continental islands exhibits the main features of the parasite fauna of the neighbouring continent. Although the separate aphid-parasite food chains are less in number of parasite species, the main scheme of such food chains remains the same both in the island and in the neighbouring continent.

In the oceanic islands, on the contrary, the fauna has no relative indigenous fauna in the neighbouring continents. It is composed of elements of various origin, which form peculiar food chains. Although there may be a certain similarity due to the influence of the main, although at a far distance occurring continental fauna, the oceanic fauna continues to exhibit peculiar island features.

In the biological control of aphids by parasites in continental islands generally the same rules as in the continents can be applied.

Oceanic islands (in the tropics namely) exhibit peculiar features that allow a wide selection of parasite species to be introduced.

— *Review.* Biological control of aphids by parasites in islands does not represent a widely distributed trend. This state corresponds naturally to the world level of applying the aphidiid parasites as control agents, which may be mentioned as a trend of the present day, if some cases of the past years are omitted.

Biological control activities have been really undertaken in Hawaii and Tasmania, while only the basic research or projects of biological control, etc., have been known in the other islands.

— Tasmania — Substantial success in biological control of the callaphidiid aphid *Tuberculoidea annulatus* by the introduced aphidiid parasite *Trioxys pallidus* from Europe (Gr. Britain) is mentioned by DERACH (1962).

— New Zealand — Only few records on aphid parasites are known from this area, although aphid fauna research has been on a good level.

Biological control of aphids in this area would be rather interesting, and it would be important to know the biological control peculiarities in the southern hemisphere temperate zone.

— Hawaii — Hawaii has been generally mentioned as a typical "biological control country" of the tropics of the Pacific area. This is also true as to the aphid parasites as agents of biological control.

The research of the aphid fauna has been continued since about the beginning of the century, some records on aphid parasites being simultaneously mentioned. The level of basic research has enabled valuable records to be obtained on the spread of immigrants—both pest aphids and parasites—over the Island.

In 1917 a *Trioxys* species was introduced from California, nevertheless, no successful recovery followed.

In 1913 an *Aphidius* and *Lysiphlebus* species were introduced from Japan to Hawaii, but no recovery has been made (SWEZEY, 1931).

In 1923 *Lysiphlebus testaceipes* was successfully introduced from California and has become successfully established over the Island, attacking a number of different aphids (FULLAWAY, 1924).

In 1960 *Aphidius smithi* was introduced from California and has become successfully established (DAVIS, 1961, etc.).

In 1965 an introduction of *Lysiphlebus testaceipes* from Mexico was made for control of *Aphis nerii*.

Besides these parasites a number of aphid predators have been introduced in the present days.

Hawaii may be characterized as an area of apparently useful possibilities of aphid control by parasites. Of oceanic island character, the tropical climate, composition of aphid fauna, and the level of basic research both of aphids and parasites represent a good field for biological control activities. The biological control in Hawaii, besides its direct economic significance for the Hawaiian area, would be rather useful as an example of biological control of aphids by parasites in tropical oceanic islands. All presumptions seem really to be at hand.

The comparison of some neighbouring islands has shown that biological control of aphids would probably be rather useful there as in the case of Hawaii. For example, SWEZEY (1942) has reported *Aphis gossypii*, *Rhopalosiphum maidis*, *Aphis nerii*, ? *Pentalonia nigroervosa*, and some other aphids, from Guam island, while an *Aphelinus* parasite has been mentioned. In this case, the introduction of some parasite species of the "*Aphis*" group parasites could be useful.

- Cuba - Its climatic characteristic is almost tropical, with the corresponding aphid fauna. The number of aphid species ascertained in Cuba is comparatively high (over 70 species found by HOLMAN, unpubl. communication), nevertheless, the number of pests is much lower. They are: *Aphis craccivora*, *A. gossypii*, *A. spiraeicola*, *Brevicoryne brassicae*, *Cerataphis* spp., *Hysteroneura setariae*, *Lipaphis pseudobrassicae*, *Myzus persicae*, *Pentaloma nigronervosa*, *Rhopalosiphum maidis*, *Siphia flava*, *Toxoptera aurantii*.

Biological control activities have been undertaken recently by the author in collaboration with Cuban workers. In the first phase of the research, basic research with respect to biological control was made, the following results being obtained: Taxonomic research of the group in Cuba (description, distribution, habitat, host specificity, world host range, hosts and localities in Cuba, notes on the economic significance), key to the genera and species, host specificity, seasonal history, foci in nature, origin of fauna, natural limitation. Biological control problems have also been dealt with, resulting in elaboration of biological control projects of the main aphid species, economic pests (STARÝ 1967). Further work in applied biological control should follow.

Lysiphlebus testaceipes material from Cuba has been experimentally introduced into Czechoslovakia (laboratory) for biological control of aphids in greenhouses of the temperate zone, and biological control of some pest aphids in some subtropical areas.

The results obtained in the research of aphid parasites of Cuba seem to be applicable also to other islands of the Caribbean. The composition of the aphid fauna of Puerto Rico (SMITH et al., 1963) at least shows a striking resemblance, in other islands the aphid fauna may be poorer, while the pests remain probably the same (sugar cane, citrus growing, etc.).

- *Analysis of successes.* Generally, we have comparatively little to analyse, practically only three successful introductions—that of *Lysiphlebus testaceipes* and *Aphidius smithi* into Hawaii, and *Trioxys pallidus* into Tasmania.

Aphidius smithi is mentioned as being highly effective and the introduction is classified as a spectacular case of biological control. In this case, the combination of tropical climate (influence on aphid and parasite biologies), perennial character of the community (alfalfa) and useful biological features of the parasite species seem to be responsible for a similar success.

Lysiphlebus testaceipes, although being successfully established in Hawaii, does not seem to reach such an effectiveness. Multiple introductions will apparently be necessary for the control of pest aphids in the island.

Trioxys pallidus is mentioned as substantially successful in controlling the callaphidid aphid *Tuberculoides annularis* in Tasmania (see DEBACH, 1962).

Summarizing, there is little material to show whether the biological control of aphids in islands is economically valuable or not. This state corresponds to the research level. Nevertheless, biological control is principally the same in continents as in the islands, so that we have to expect that the research will successfully develop and further valuable results such as those that have been obtained in the past and the present day will be reached in various countries

- Aphids - control objects -

Acyrtosiphon pisum

Parasite: *Aphidius smithi* In Hawaii, introduced 1960, outstandingly effective.

Aphis craccivora

Parasite: *Lysiphlebus testaceipes*. In Hawaii, introduced 1923, partially to substantially effective.

Aphis gossypii

Parasite: *Lysiphlebus testaceipes*. In Hawaii, introduced 1923, partially to substantially effective.

Aphis nerii

Parasite: *Lysiphlebus testaceipes*. In Hawaii, introduced 1965, substantially effective (in natural enemy complex).

Longimignis sacchari

Parasite: *Lysiphlebus testaceipes*. In Hawaii, introduced 1923, substantially effective in natural enemy complex.

Rhopalosiphum maidis

Parasite: *Lysiphlebus testaceipes*. In Hawaii, introduced 1923, partially successful.

Toxoptera anrantii

Parasite: *Lysiphlebus testaceipes*. In Hawaii, introduced 1923, partially to substantially successful.

Tuberculoides annulatus

Parasite: *Trioxys pallidus*. In Tasmania, introduced 1939, substantially successful.

According to these records substantial to outstanding results have been obtained through introduction of various parasite species in island areas.

~ Parasites - control agents -

Aphidius smithi

Aphid: *Acyrtosiphon pisum*. In Hawaii, introduced 1960, outstanding effectivity.

Aphidius sp.

Aphid: "Aphids". In Hawaii, introduced 1913, unsuccessful establishment.

Diaeretiella rapae

Aphid: *Brevicoryne brassicae*. In Hawaii, introduced 1902.

Lysiphlebus testaceipes (Hawaii - 1923)

Aphid: *Aphis gossypii*, *A. craccivora*, *Rhopalosiphum maidis*, *Longimignis sacchari*, *Toxoptera anrantii*. Introduced 1923, partially to substantially successful.

Lysiphlebus testaceipes (Hawaii - 1965)

Aphid: *Aphis nerii*, in Hawaii, introduced 1965. Effectiveness: No records as yet.

Lysiphlebus sp.

Aphid: "Aphids". In Hawaii, introduced 1913, unsuccessful establishment.

Trioxys pallidus

Aphid: *Tuberculoides annulatus*. In Tasmania, introduced 1939, substantially effective.

Trioxys sp.

Aphid: "Aphids". In Hawaii, introduced 1907, unsuccessful establishment.

The results have been classified as outstanding, substantial and partial, according to DEBACH (1962).

- Hawaii - an example of biological control - The history of biological control of aphids by parasites in Hawaii has fortunately been connected with the world level of this research. Because of its suitable tropical climate and oceanic island character, rapid progress of agriculture, etc., it has become an area of intensive entomology research work in many directions. The research of island fauna was very deep and careful, and this has enabled the registering of new immigrants, their gradual spread over the island, damage caused to plants by new pests, etc. These activities have been in progress up to the present day, representing a value of many years experiments.

The research of aphids and then the research of their natural enemies was practically begun at the beginning of the century (FULLAWAY, 1912, TIMBERLAKE, 1918, etc.). It was soon recognized that aphids represent an important group of insect pests and biological control activities resulting in introductions of parasites from abroad began.

In 1907 a *Trioxys* species, a parasite of an orange aphid, was sent from California to Hawaii (SWEZEY, 1931). No recoveries of this parasite were made.

In 1917 an *Aphidius* and *Lysiphlebus* species were introduced from Japan to Hawaii, however, this experiment was unsuccessful as well (SWEZEY, 1931).

Both the biological control activities of 1907 and 1913 were apparently a result more of enthusiasm than true research work activities as there were no records on the biology, hosts, etc., nor taxonomic identification of the species. The records like "parasite of plant lice" show that there was a poor knowledge of the significance of host specificity, etc., of the parasites, these being probably supposed to be "polyphagous". This state was in agreement with the corresponding ideas of the group at that time.

In 1923 *Lysiphlebus testaceipes* was sent from California to Hawaii (FULLAWAY, 1924, SWEZEY, 1931), parasitizing *Aphis gossypii*, *A. craccivora*, *Toxoptera aurantii*. P. H. TIMBERLAKE has sent this parasite in numbers from California for colonization in Hawaii. This selection must be classified as of first class quality as to the idea. TIMBERLAKE has apparently selected accidentally this species, nevertheless, it is just one of the species which are extremely both widely specialized and distributed, covering some areas of the temperate, subtropic and tropical zone. The colonization of the parasite has been successful and the species soon spread over Hawaii and the allied islands:

Lysiphlebus testaceipes, its introduction and spread in Hawaii (1923-1946).

1923, introduced from California (FULLAWAY 1924), (Notes and exhibitions, 1924).

1927, *Rhopalosiphum maidis* (TIMBERLAKE, 1927; hyperparasites in Hawaii ascertained).

1928, *Aphis* sp. on *Phaseolus* (Notes and exhibitions, 1928).

1929, *Longitarsus sacchari* on sugar cane (Notes and exhibitions 1929), in a greenhouse(!).

1929, *Aphis craccivora*, in Molokai (SWEZEY & BRYAN 1929).

1929, *Aphis gossypii* (ILLINGWORTH, 1929).

1931, aphids on Hibiscus (Notes and exhibitions, 1931).

1941, *Aphis gossypii*, Isl. of Midway (BIANCHI, 1941).

1946, *Rhopalosiphum maidis* (HOLDAWAY & NISHIDA, 1946).

1946, *Rhopalosiphum maidis* (Notes and exhibitions, 1946) (mentioned to be effective, nevertheless did not prevent the heavy infestation of new corn plantings, so that insecticidal control of the aphids was necessary.)

1965, another stock introduced from Mexico to control *Aphis nerii* in Hawaii.

Although this parasite is rather effective, it seems that it has not become so effective as to prevent aphid outbreaks. According to our opinion, introduction of other parasites is recommended.

In 1960 *Aphidius smithi* was introduced from California to Hawaii (DAVIS, 1961, Annual Report, 1960-61, BEARDSLEY, 1961, etc.), and it became established in the following years (Annual report, 1963), etc. Being of Indian origin, it has been introduced, colonized and successfully established in California, where it is a rather useful control agent of *Acyrtosiphon pisum*. Similarly, in Hawaii, the success was reported as spectacular (F. J. SIMMONDS, unpublished communication, autumn 1966).

In 1965 *Lysiphlebus testaceipes* was sent to Hawaii from Mexico for biological control of *Aphis nerii* (Annual Report, 1965). As far as we can judge from the literary record, strangely enough the *Lysiphlebus testaceipes* stock colonized in 1923 did not cover the mentioned aphid either, as it attacks this species in California, Cuba, etc.

- *Significance of faunal research* Theoretical presumption as well as some practical results have shown that biological control of aphids in islands—for example in the

subtropics and tropics—seems to be useful in biological control. The basic research of the fauna has resulted in obtaining valuable records on the peculiarities of island fauna, connections between the various continents—migration routes of the parasite fauna, spread of parasites, etc. The research has also enabled the obtaining of records on possibly valuable material for the exportation abroad of certain parasite species.

The following islands have served as sources of material for parasite exportation abroad:

Br. Isles. *Trioxys pallidus* has been exported for biological control of some Callaphidid aphids to Tasmania.

Japan. In 1913 *Aphidius sp.* and *Lysiphlebus sp.* were exported to Hawaii. In recent years, search for Citrus aphid parasites as well as other parasites in Japan and in neighbouring areas (S. Korea, etc.) has been undertaken by the California research workers, some aphidid species being exported to California insectaries. Similar activities were undertaken in the thirties.

Taiwan. The island was covered by the search for aphid parasites organised in Far Eastern countries (see above).

Both the lack of the comparison of biological features of parasite populations from the continents and relative islands as well as the comparatively poor knowledge of specific composition of the given faunas (Far East) do not allow us to mention and stress any features typical for certain island populations. Judging from our studies undertaken in Cuba (1965) which—as to its relation to the continental N. America—represents a similar case, the specific composition of parasites and some data on their biologies being better known, some differences might occur. Although Far Eastern districts—including islands—represent one center of the aphidid group development, some species occurring there are of another origin and they might possess certain biological peculiarities.

Unfortunately no material of parasite populations was exported from an oceanic island to ascertain the changes in parasite host specificity, habitat preference, etc.

— ISLAND PECULIARITIES (FIG. 320). It is necessary to know the main data on the taxonomy, origin, distribution, habitat, biology, and injury caused to host plants by the pest aphid species. On this base we can estimate which host plants, in which habitats, etc., the new pest aphid will attack, how it will spread over an island. Similarly, general knowledge of the aphid biology in separate climatic zones is useful.

A crop is often newly introduced in an island. We can expect that such a crop will be attacked by an aphid pest: this pest may be a polyphagous species that occurs in the island, but we can also expect—due to the factors influencing the aphid dispersal—that a new pest will soon appear. In case of the occurrence of a specialized pest aphid, theoretical knowledge of the control is necessary, at least in general features in order to introduce suitable parasite species for its control to prevent outbreaks and extensive damage of plantations. For example, alfalfa has recently been grown on experimental plantations in Cuba as a forage crop. Although in 1965 no typical pest aphid occurring on these experimental plots was found (*Acyrtosiphon pisum*, *Therioaphis trifolii*), we can expect that these pests will soon appear in Cuba—when the alfalfa crop is grown more extensively—due to the close neighbourhood of C. America, Florida, etc., where the pests are distributed as well as in other parts of the Nearctic America. For this reason, a biological control program has been elaborated for these pests, too (STARÝ 1967 etc.).

— Parasites. A historical approach to the introduction principles is necessary. The first classification must be that of the type of island. Oceanic and continental islands exhibit different features as to the plant communities, which is of basic importance for the presence of parasite species. In the case of a continental island there will be

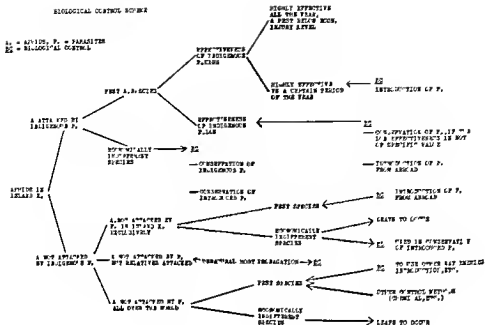


Fig. 320. Aphids and parasites in islands.

present at least some members of faunistic complexes of parasites corresponding to separate main floristic zones. In the case of an oceanic island, the fauna of parasites will be composed of accidentally immigrant species, members of various faunistic complexes. The climatic zone has also a great influence in a given island.

Further, the probable response of indigenous island species to the newly introduced pest aphid may be preliminarily classified, in connection with the taxonomical-ecological features of the pest aphid given and the host specificity range of the indigenous parasites. In some cases, some parasite species may be simultaneously (accidentally) introduced with the pest aphid; their establishment, effectiveness, etc. in the new environment must also be considered.

Selection of parasite species to be introduced will depend on the classification of the island again. In the case of a continental island, we have to deal with historically developed faunistic complexes of native parasites, and these complexes must then be complemented by a newly introduced parasite species. On the contrary, in the case of oceanic or almost-oceanic islands, no faunistic complexes are present, but the fauna is in evolution: here we can carefully select and introduce a parasite species from abroad. Oceanic islands in the tropics seem to be most suitable due to the comparatively low number of pest species present, the common gaps in natural limitation of aphids and to the biological features of aphids and parasites in these areas.

Various viewpoints and aspects have been thrown on the problem of multiple introduction by various biological control workers (see DEBACH & SUNDBY, 1963, etc.). In island conditions any introduction has naturally to be well classified to prevent any mistakes. In our opinion the principal task has to be used as the primary point of view: the pest aphid must be kept under control throughout the whole year, no gaps in parasite effectiveness enabling pest outbreaks.

This means that in case of a well specialized parasite, which will be found to be useful enough in the above mentioned way, no other introductions will probably be

necessary. For example, *Acyrtosiphon pisum* has become a serious pest of alfalfa in Hawaii. The introduction of the parasite *Aphidius smithi* has given splendid results, the single parasite species keeping the pest under control in this case.

Nevertheless, in case of certain widely polyphagous aphid species that occur in a number of habitats and in various seasons, a single parasite species will probably hardly be able to control the pest successfully. More species must be introduced. There is no danger of interspecific competition that would be dangerous as to the effects of biological control. As far as we can judge from the cases of incidental immigrants and their interspecific competition in various islands (Cuba, Hawaii), it seems that more progressive species will be more successful in such a competition, as e.g. *Lysiphlebus testaceipes* in Cuba, while the other species will apparently remain in a lower population density level. In our opinion, if the species introduced become successfully established, they can be expected to select naturally the most suitable habitats as well as the best season for their occurrence, and all these features are dependent specifically and usually differ from each other.

The problem of host range has also often been discussed by various specialists. Monophagous species are more advantageous in having the possibility of good synchronization with the host occurrence if suitable environment occurs. Nevertheless, they may fail to establish, in case of a poor synchronization occurrence, as they have no possibility of successfully attacking any alternative host. In island conditions, there is a possibility that also the species that are not strict specialists in their native home, will be forced by lack of other suitable hosts in an island environment, to behave as if being monophagous there. This seems to be the case of *Acyrtosiphon pisum* and *Aphidius smithi* in Hawaii. Widely specialized parasite species, on the contrary, possess the ability of attacking the other host species if present in the island, and thus to survive periods of one pest aphid absence, nevertheless, there may be less synchronization with the occurrence of the pest aphid to be controlled, due just to the wide range of host specificity of the parasite. In our opinion, the widely specialized parasites can be generally classified as a very useful species owing to several reasons: our observations from Cuba show that the pest aphid usually occurs in a number of communities, both of a natural and cultivated type. It has therefore to be controlled in these communities, and the widely specialized parasite is perhaps more suitable for the task, being able to occur in separate communities independently of the given pest aphid presence.

For example, *Lysiphlebus testaceipes* has been originally introduced into Hawaii for the control of *Longiunguis sacchari* (DEBACH, 1962). Nevertheless, in the following years it was found to attack, besides *Longiunguis*, also a number of other aphid pests (*Aphis craccivora*, *A. gossypii*, *Rhopalosiphum maidis*, etc.).

In some cases, and this is just true for the oceanic islands of the tropical zone, there are several species of aphid pests which belong to the same similar taxonomical-ecological type, thus being parasitized by a group of widely specialized parasites simultaneously. For example, the main pest aphids (in addition to others) in Cuba are *Aphis craccivora*, *A. gossypii*, *A. spiraeicola*, *Rhopalosiphum maidis*, *Toxoptera aurantii*, all of which belong to the "Aphis" group, so that a certain parasite species may cover them all in their host specificity range simultaneously—as just *Lysiphlebus testaceipes* does now in Cuba in an accidental way (immigrant). In a similar case, several pest species can be covered simultaneously by introducing one widely specialized parasite species.

Careful quarantine of introduced material is necessary, to prevent the introduction of hyperparasites.

—Colonization. A careful classification of the environment is necessary both to select the

best place for a colonization site and to presuppose the further spread of the parasite over an island with respect to its habitat requirements. Main crops as well as weed plants must be reviewed in relation to the pest aphid and parasite occurrence. Indigenous aphid fauna may also play a rather important part. Besides the pest species that has to be controlled, the other aphid species may also be useful; some of them may be entirely indifferent, being omitted by the parasites, the others may represent alternative hosts of the parasites, thus being valuable for biological control. Such indifferent types of aphids may be useful in enabling the parasite's survival of the period of the pest aphid absence in a given area.

Hyperparasites, representing apparently mostly widely specialized species, may be expected to attack the introduced parasite very soon, representing one of the important factors relatively lowering the parasite effectiveness in an island.

For example, *Lysiphlebus testaceipes* was successfully introduced in Hawaii in 1923, and became well established in the following years, attacking a number of aphid species. Nevertheless, in 1927 it was reported as being hardly capable of fully controlling *Rhopalosiphum maidis*, an important virus vector on sugar cane, as "unfortunately there are already present in the Island several secondary parasites of aphids, which would lessen the efficiency of any internal parasites" (TIMBERLAKE, 1927).

—*Conservation.* The conservation of aphid parasites—both indigenous and introduced species—is undoubtedly an important problem.

The problem of conservation depends basically on the object, i.e. is a specifically dependent phenomenon. For this reason an example is mentioned here to show the principles of the problem.

The principal seasonal difficulty in biological control experiments is the survival of the parasites during a certain period of their main host absence; further, the foci of parasites in nature, from where they may spread to the crops in case they are seasonally attacked by pest aphids. In tropical oceanic islands this phenomenon appears to be important. Although a tropical climate causes comparatively advantageous features of aphid biology, the influence of dry and wet yearly seasons may be different in different communities. In a number of crops the role of the parasites is important—when they are able to spread and occur in the infested field. Their ability to parasitize the aphid depends on the sources in the environment, on the presence of their alternative hosts, etc. Similarly, the occurrence of suitable alternative hosts in various habitats represents simultaneously a presumption for the occurrence of parasites, which may (and they do so) attack the pest aphids present in the given habitat. A proposal therefore may be mentioned to use the common indifferent aphid species occurring in widely distributed plant species in parasite conservation. *Nerium oleander*, being commonly and practically attacked throughout all the season by *Aphis nerii*, represents such a case. As an ornamental, it is grown practically everywhere. Although a certain (often serious) damage is caused to this ornamental by the aphid, we suppose that the advantage of the aphid occurrence as an alternative host of *Lysiphlebus testaceipes* seems to be much higher. Our opinion, although based on field observations only (Cuba 1965), is supported by the comparison of the importance of a number of pest species attacked by the parasite mentioned in Cuba (*Toxoptera aurantii*, *Aphis spiraecola*, *A. craccivora*, *Rhopalosiphum maidis*, etc.) with the economic significance of *Aphis nerii* as a pest of *Nerium oleander* ornamental.

—*Aphid-vectors.* The parasites generally lower the population number of aphids that can transmit a virus disease from one plant to another as they mostly kill the aphids before they reach maturity. Nevertheless, they are unable to eradicate an aphid species, owing to several reasons—one of them is the action of hyperparasites—

in the frame of community equilibrium level. This means that also in the case of their high effectiveness a certain number of aphids remain untouched, as the primary parasites peak is soon followed by the peak of hyperparasites. However, although aphid eradication never follows, the primary parasites are important as also in case of hyperparasitism the given aphid represents a killed specimen. The incapability of the primary parasites to destroy completely the aphid population-vectors have been recognized just in island conditions (Hawaii) by TIMBERLAKE (1927) in the case of *Rhopalosiphum maidis*: "The corn aphid has recently received attention, after the discovery that it carries the mosaic disease from grasses and corn to sugar cane. The control of this aphid to such an extent that it will no longer be feared as a carrier of disease, is, I am afraid, an impossibility. Unfortunately, there are already present in the Islands several secondary parasites of aphids, which would lessen the efficiency of any internal parasite and even if a ninety or even ninety-five per cent control could be brought about, this probably would not be sufficient to prevent the aphid from spreading the disease".

— *Weeds*. With respect to biological control, the weed plants may be divided into the four following groups:

1. Weeds not attacked by aphids.
2. Weeds attacked by aphids that are economically indifferent, not being infested by parasites at all or attacked by indifferent parasite species. Examples: Cuba. Weed: *Erigeron canadense*. Aphid: *Dactynotus erigeronensis*. Parasite: *Aphidius floridaensis*, rarely *Lysiphlebus testaceipes*.

Weed plants of the two groups mentioned are indifferent from the point of view of biological control of aphids (by parasites).

3. Weeds attacked by aphids that are pests of economic crops. Example: Cuba. Weed: *Eupatorium* sp. Aphid: *Aphis spiraeicola* (mainly), *Toxoptera auranti*, *Neomyzus circumflexus*. Parasite: *Lysiphlebus testaceipes*. Cuba. Weed: *Ruellia paniculata*. Aphid: *Aphis gossypii*. Parasite: *Lysiphlebus testaceipes*.

Weed plants of this type are rather dangerous. They represent food plants for pest aphids, where the latter feed during certain periods and spread again from these to the crops. For example: *Eupatorium* sp.—a common weed in Citrus and other orchard undergrowth in Cuba—is the preferred plant of *Aphis spiraeicola*, which is a serious seasonal pest on Citrus. In certain areas such weeds can be killed by herbicides, nevertheless, biological control seems to be more valuable covering the aphids on untreated areas as well.

4. Weeds attacked by aphids that are economically indifferent, but represent alternative hosts of useful parasite species.

Examples: Cuba. Weed: *Bidens pilosa*. Aphid: *Aphis coreopsidis* (mainly), *Acyrtosiphon bidencicola* (indifferent species), *Aphis spiraeicola* (rarely). Parasite: *Lysiphlebus testaceipes*. In this case, the role of the weed during certain seasons seems to be extremely important for parasite survival and conservation.

Cuba. Weed: *Callotropis procera*. Aphid: *Aphis nerii*. Parasite: *Lysiphlebus testaceipes*. In this case, *Aphis nerii* is a preferred host of the parasite during the greatest part of the season. The damage caused by the aphid to the ornamentals (*Nerium oleander*) seems to be overlapped by the significance of the aphid as a host of effective parasite species, which attacks a number of pest aphids. *Callotropis procera* in Cuba can be found in pasture meadows, waste places, from lowlands to mountains. It seems to be very important in representing sources of alternative host of *L. testaceipes* in very dry and hot areas, where the other aphids are very scarce at least during some parts of the season.

From the economic point of view, weed plants have to be classified as all plants,

the presence of which is not necessary in the given cultivated area. For this reason, we have to distinguish between the occurrence of weeds in the fields and on ruderal and other places. Weeds in cultivated areas today mostly may be easily controlled by herbicides. Otherwise, weeds may commonly be found along the roads, in ruderals, balks, pastures, meadows, orchard undergrowth, gardens, etc. All these places are usually uncontrolled or uncontrollable. Weed plants then represent, if the above mentioned classification is used, either indifferent plants, or sources of (a) pest aphids, (b) indifferent aphids, (c) aphids useful for parasite propagation. Because of the poor control possibilities in various places, their significance as sources of the mentioned aphid fauna must be stressed; just in such places, the aphid limitation by natural enemies is very important.

- *Greenhouses.* The same seems probably to be true of the biological control of aphids in greenhouses in continental as well as island areas. In the (oceanic) islands, however, the number of parasite species is lower, and this may probably influence the natural sources of the parasites invading the greenhouse from the neighbourhood.

No detailed records are known. Only one very interesting record can be mentioned. In 1923 (see above) *Lysiphlebus testaceipes* was introduced and successfully established in Hawaii. In 1929 this species was reported as a parasite of *Longiunguis sacchari* on sugar cane in a greenhouse. In this case, the biological control introduction accidentally covered a part of the biological control in greenhouses (tropical environment peculiarities).

REFERENCES. 12-15, 60-1, 62, 77, 86, 190, 192, 210, 235-6, 251, 295, 336, 432-5, 535, 545, 567, 568, 763, 804-5, 829-34, 876, 1055, 1134, 1162-3, 1165-75, 1176, 1266.

GREENHOUSES. Greenhouses, as practically closed environments, have been dealt with by a number of authors with respect to biological control possibilities. As there was no possibility of escape for a pest owing to restricted space, biological control seemed to be a very easy matter in introducing natural enemies into the greenhouse environment in order to control the pest. As aphids represent common pests in greenhouses, the same as the coccids or aleyrodids, they represented a relatively common object of biological control. Moreover, the natural enemies were believed to represent a continuously present regulating agent, while it was necessary to repeat the treatments many times in the course of the year.

- ENVIRONMENT. Greenhouses are typical artificial environments. Conditions that occur in a greenhouse differ very considerably from the conditions of the neighbourhood, either the plant species grown are quite different, or the plants although identical are in a different developmental stage owing to different temperature conditions.

Heated greenhouses represent perennial environments, although the conditions change within certain limits during the season. Unheated greenhouses are seasonal environments being used in early spring to grow crops earlier than under natural conditions.

According to their purpose, greenhouses can be divided into several groups: experimental greenhouses are usually smaller, for the use of research institutes for plant growing or even as insectariums. Their plant composition depends on the experimental program. Ornamental greenhouses include extensive greenhouses of botanical gardens as well as smaller ones that serve as a winter environment of various room plants as can commonly be found everywhere. These greenhouses often represent very old environments, where the culture of plants has occurred for many years. Finally, there is an extensive group of economic greenhouses, where

both ornamental plants and economic crops such as fruit and vegetables are produced in quantities; the production is practically perennial, but the plant species can change depending on the season. Naturally, there are a number of intermediate types.

A greenhouse community, which develops in an artificial environment, is an artificial community, which has developed from introduced species of cosmopolitan or less widely distributed common greenhouse pests, and from the out-of-doors fauna that invades a greenhouse. Naturally, the food chains which develop in consequence are often artificial and incomplete. The number of species is low, although their population number can be numerous. These features make the community of a greenhouse rather unstable and outbreaks of pests can often be observed. Only relatively stable communities can be found in rather old botanical gardens but even here they are far from being the relative completeness of natural environments.

Aphids, as plant feeding insects, are a typical group that occur in greenhouse environments. The aphid species of tropical origin for example found the conditions rather favourable for most of the year, as they resemble the conditions of their native country, the tropics. These species have become widely distributed cosmopolitan greenhouse pests. Many species that occur in greenhouses are also indigenous species on a given area that have invaded the greenhouse environment from the open.

Contrary to aphids, parasites that are found in greenhouses mostly represent indigenous species which have invaded the greenhouse environment from the neighbourhood. No cosmopolitan species are known to spread in a similar way as the tropical aphid species. Certain strains, however, that are not capable of surviving in the open are known in some areas (California, *Aphidius matricariae* greenhouse strain, SCHLINGER & MACKAUER, 1963).

Greenhouse conditions also change according to the season, although these changes are different from those in the open. Late autumn, winter and early spring conditions, when the greenhouses are heated and the temperature must be more or less controlled because of plant requirements, they are more or less constant, while spring, summer and early autumn conditions may be unfavourable as the temperature can rise very considerably. The photoperiod is identical with the outside, but the combination of a short photoperiod in the winter months, favourable temperature and growing plants make greenhouse conditions quite different from those out in the open.

— GENERAL PROBLEMS. The problematics of aphid control in greenhouses can be briefly characterized as follows: greenhouse conditions are, with the exception of the summer period, generally rather favourable for the increase of pest aphid populations. Plant growing in greenhouses is very intensive. The aphids may attack many plant species or they may be restricted in food range. Different plants respond quite differently to various insecticides. Generally, greenhouse plants are more sensitive than in natural stands. There is the problem of residues in a greenhouse, both in plants and soil, as well as with respect to human health. Chemical treatment is known not always to eliminate the aphids, although several insecticides may be used either simultaneously or gradually, aphid pests survive although in low numbers, and rapid increase in numbers soon follows after treatment so that a new treatment must begin. Mostly there is a lack of aphid natural enemies in greenhouses; widely accepted chemical control is probably responsible for this condition too as it seems to eliminate even the accidental invaders from the open. Biological agents in aphid control are probably useful as they could be capable of keeping the aphid populations on subeconomic levels. It is, however, very difficult to eliminate the aphid pests from greenhouse environments completely.

The aphids cause damage to greenhouse plants in their usual manner; the sucking of the aphids causes weakening and even the drying of plants and naturally their

development is less favourable; honeydew production is highly unfavourable just in greenhouses as the fungi develop very intensively under wet greenhouse conditions. Deformation of plants due to aphid feeding is also common, the young shoots are attacked for instance and virus transmission plays also a role. The significance of the various types of damage caused depends on the kind of production; for example, plants in botanical gardens can survive the honeydew cover for a certain period, while the same intensity makes the flowering plants less valuable for the market.

– **BIOLOGICAL CONTROL.** Pest aphids that occur in (heated) greenhouses can be divided into two groups: first, there are practically cosmopolitan species, mostly of tropical origin such as *Myzus persicae* (tropical strain), *Neomyzus circumflexus* and others; in these groups also less common species belong such as *Sitobium luteum* and *Cerataphis* spp., *Toxoptera aurantii* and others. In the second group species can be included which are out-of-door invaders of the greenhouse neighbourhood; their species composition depends on a given community; we may find *Aphis hederæ*, *A. craccivora*, *Macrosiphum rosae*, *Rhopalosiphum maidis*, etc.

With the exception of *Cerataphis* spp., which are not attacked at all by aphid parasites, all the aphids that occur in greenhouses are known to be attacked by an aphid parasite at least in a certain part of their known distribution area. A cosmopolitan species must be controlled by a selected species, while the indigenous aphids that invade a greenhouse from the neighbourhood may be controlled by their indigenous parasites which attack them in the open. For example, TRIPLEHORN (1962) considers *Rhopalosiphum maidis* to be a constant problem in Ohio, U.S.A. greenhouses where plantings of corn or sorghum are grown during the winter. We have reared this species in a heated greenhouse in Czechoslovakia on corn and the control by the introduced Cuban population of *Lysiphlebus testaceipes* was effective. With respect to aphid specificity, we again can recognize several groups. Perhaps the most injurious are the polyphagous species as *Myzus persicae* or *Neomyzus circumflexus*, while another extreme represents species attached to certain plant species such as *Macrosiphum rosae* (Rosa), *Cerataphis* sp. (orchids), *Aphis hederæ* (*Hedera helix*), etc.

– **Parasites – control agents.** Because of the closed environment, even a wide host range of a parasite becomes restricted in a greenhouse, the parasite attacking only a single or a few hosts from its wide host range. Consequently, even a widely specialized parasite may behave as a monophagous species in a greenhouse. For example, *Aphidius matricariae*, because of the lack of other hosts, may attack only *Myzus persicae* in greenhouse conditions. On the other hand, parasites can attack several hosts if these are present in a greenhouse environment. For example, in our experimental greenhouse, the introduced Cuban population of *Lysiphlebus testaceipes* attacked the introduced aphids, *Aphis spiraeola*, *A. craccivora*, *Rhopalosiphum maidis*, *Toxoptera aurantii*, in a similar way as in its native home. The host range is rather important; a widely specialized parasite acts in relation to aphid populations in the same way as to a single one (see below), so that it is able to control several species simultaneously. It is, however, known that the most numerous populations are attacked the most. Different temperature requirements of the separate species attacked and those of the parasite could restrict its effectiveness to some periods and, consequently, only to some aphid species as well.

– **Unnatural host propagation** – Practically, a greenhouse represents a closed space, in which the host range is restricted to the species present. Nevertheless, the parasite may meet there some hosts, the potential hosts, which cannot be met with in nature, as they are attached to the greenhouse environments (tropical origin). This possibility as well as the pressure of the environmental forces may result in attack and even a successful parasitization of a new host in the greenhouse environment, which is

classified as an unnatural host. Such a case of accidental propagation of *Neomyzus circumflexus* as unnatural host of *Diacretiella rapae* was found in our experimental greenhouse in Czechoslovakia. *N. circumflexus* is restricted to greenhouse conditions in this country and is not capable of surviving the winter in the open. It is a typically cosmopolitan greenhouse aphid, of tropical origin. Thus, the parasite populations, which were introduced from field environments to control another pest, *Myzus persicae*, had not had the possibility to meet the *Neomyzus* aphid in the open, but we ascertained several cases of successful attack and development of the parasite in this aphid.

— Host-parasite system — Greenhouse environment, where host aphid and parasite occur, may be placed as a parallel to experimental host-parasite systems, where there is no or low dispersal possibility, temperature conditions change more in closed spaces than in the open, and there is no interference from other natural enemies.

Experiments of MCLEOD (1937), based on the comparison of temperature conditions in several greenhouses with respect to parasite effectiveness (*Aphidius matricariae*, *Myzus persicae*) clearly showed that the parasite was effective only in certain temperature limits. These results are supported by the conclusions of BURNETT (1949), who made experiments on temperature-dependence of effectiveness of *Encarsia* parasites in parasitizing their aleyrodid hosts.

The lack of or low possibility of dispersal brings the selfregulation mechanisms of a parasite population into action. Under certain population numbers superparasitism can often be observed correspondingly reducing the increase of parasite population. This was observed by TIMBERLAKE (1910). The possible accidental introduction of hyperparasites could prevent superparasitism, in decreasing the population of primary parasites, but the final result would perhaps be similar.

If we omit the action of parasites and conditions of host plant, changes occur in population numbers of aphids depending on temperature. Each aphid species has an optimum temperature and it can become more or less numerous according to this. For example, if we rear *Acyrtosiphon pisum* and *Aphis craccivora* populations on beans in a greenhouse, *Acyrtosiphon* aphids develop better under a lower temperature, while *A. craccivora* reproduces quicker under higher temperatures. Consequently, as the temperature conditions change in a greenhouse during the season, the various aphid populations become more numerous in different periods of the year. It seems that late autumn to early spring conditions in a heated greenhouse are favoured best by most of the greenhouse pest aphids.

The parasite action, besides its intrinsic features, will be restricted by temperature and population density of aphid populations. As the temperature optimum of the host and parasite can differ, the parasite effectiveness can be limited by certain temperatures; for this reason, several parasite species should be introduced. Further, it depends on the parasite host specificity range whether it behaves to the populations of various aphids as to a single one (see examples of *Lysiphlebus testaceipes*) or whether its host range restricts its dependence to a single aphid species population.

— Selection of species — 1. Indigenous species. This seems to be a very easy way of controlling the aphids in greenhouses. If the same pest occurs in the open and in a greenhouse, we rear the parasites from the field colonies and transfer them to the greenhouse. Very often, the parasites themselves invade the greenhouse accidentally.

Biological control of pest aphids by their indigenous parasites seems to be prevalent in the literature. For example, WITHINGTON (1909) used *Ephedrus incompletus* in control of *Macrosiphum rosae*; BARNES (1935) controlled *Myzus persicae* by *Aphidius matricariae*; MCLEOD (1937, 1938, 1939) used *Ephedrus persicae* and *Aphidius matricariae* in controlling *Myzus persicae*. Accidental introduction of a parasite in a greenhouse was recorded from Hawaii (Notes and exhibitions, 1929) where *Lysiphlebus testaceipes*,

a species introduced from California to Hawaii in 1923 invaded a greenhouse and attacked *Longinigus sacchari* on sugar cane seedlings.

2. Introduced species. It is possible that we shall not succeed in the control of the cosmopolitan pests such as *Myzus persicae* or *Neomyzus circumflexus* by the application of the indigenous species. In this case, it would be useful to introduce other parasites from abroad. Populations or species from more southern countries would certainly be preferable.

3. Artificial and natural food chains. We have mentioned above that the community of a greenhouse is practically an artificial community, composed of cosmopolitan greenhouse pests and out-of-doors indigenous fauna invaders. Thus natural food chains, if any, occur only partially in greenhouses in case that indigenous natural enemies (parasites) succeeded in invading the greenhouse. In aphid species, which cannot occur outside greenhouses, quite artificial food chains develop accidentally. The greenhouse conditions permit us to select the parasite species carefully to cover the host both in time and space, i.e. with respect to the changes in temperature and microhabitat.

4. The number of species to be introduced into a greenhouse is rather important. We must stress in this respect that a greenhouse represents practically a host-parasite system, the environmental temperature being changeable. Changes in temperature can influence parasite effectiveness and thus allow the aphid to reach a high population under certain conditions of temperature which will be unfavourable for parasite increase. That such cases are rather probable, we can recognize from the comparison of experimental host-parasite systems and the influence of different temperatures (see: natural limitation). Thus, it is obvious that we must introduce several parasite species which support different temperatures and this could keep the pest under control throughout the year. There is still another factor, which supports a larger number of parasites being introduced, the microenvironment (see below). There is no doubt that a more numerous complex of parasites will strongly support the stability of the greenhouse community with respect to aphid populations.

- Microenvironment. Multilateral control - The significance of the microhabitat in parasite specificity is well known. In nature, various members of the food chains occur, each of which attacks the aphids in different or in certain restricted microhabitats, so that the aphid is attacked by the natural enemies in practically all the microenvironments in which it occurs. It is quite another situation in artificial greenhouse conditions. A given aphid species occurs in different microhabitats: it can occur in more shady or more exposed situations, or the shape of the colony may depend on the plant species attacked. If the parasite is not able to attack the aphid in all microhabitats, the aphid may successfully reproduce in certain microhabitats and can reach outbreak numbers here or at least continuously disperse from there to other places, the possibility of outbreak being continuously present in a greenhouse. We can give an illustration of this with two examples: MCLEOD (1937), when controlling *Myzus persicae* by parasites, ascertained that *Ephedrus persicae* attacked only aphids living on more exposed parts of the plant, while *Aphidius matricariae* preferred more shady situations. It is obvious that each single parasite would not be able to control the aphid under all situations. We observed a similar situation in a greenhouse in Czechoslovakia. We have purposely introduced *Diaeretiella rapae* to control *Myzus persicae*, the parasite, however, was extremely successful in parasitizing the aphid colonies occurring only on large flat leaves, while colonies of the aphid that developed around a plant stem (on Bougainvillea or Asparagus) were practically omitted. Thus the principle of aphid control in a greenhouse must be multilateral in covering the aphid pest in all microhabitats.

— Methods — 1. Release of introduced species seems to be a very easy method. Aphids which belong to the hosts of the selected parasite species are collected in nature during the season, grown in a Petri-dish or another cage and the emerged adults are collected and transferred to the greenhouse. Care must be taken when selecting the primary parasites to avoid the introduction of hyperparasites. If, however, unsuitable conditions prevail in the greenhouse during the given part of the season when the parasites may be collected in the open, we can rear the aphids and parasites as a laboratory stock (see biological control program) and transfer the parasites into the greenhouse at a more favourable period: thus, parasites collected during the spring or summer months may not be used earlier than in the autumn, etc. It is recommendable to introduce a larger number of parasite adults. All the adults can be either transferred into an aphid colony, or closed together with the aphid colony inside a nylon sack for about one day; this supports the concentration of parasites and a more favourable development of the introduced population in its early stage.

2. Artificial foci, introduction of alternative hosts are another method, which could be more useful for less specialized workers. The basic feature of such a host is that it does not attack the greenhouse plants and eventually it becomes a new pest. We have developed this method with respect to the control of *Myzus persicae* in our heated experimental greenhouse in Czechoslovakia: in the autumn, a variety of Brassica crops is grown and harvested and used as a fodder crop. The crop is commonly attacked by *Brevicoryne brassicae* populations. In the autumn, practically every colony of the aphid is attacked by *Diaeretiella rapae* to a certain degree. The parasite attacks *Myzus persicae* as well. *Brevicoryne brassicae* is useful in being restricted to Brassica crops. Thus, we potted several plants infested by *Br. brassicae* and transferred them to the greenhouse. After several days, the mummified aphids—as we had expected—appeared inside the colonies and later the parasites emerged. Although they concentrated on *Br. brassicae* as a preferred host, they also attacked *Myzus persicae* on broad leaves of various greenhouse plants. Later the *Br. brassicae* colonies were so heavily parasitized that the aphid became very scarce and the parasite populations mostly developed in the *Myzus persicae* population. This method is very easy, but hyperparasites may be also introduced. It is still a question, whether the hyperparasites are useful for the regulation of a primary parasite population in a greenhouse environment or not (Fig. 321).

— GREENHOUSES AS TOOLS FOR BIOLOGICAL CONTROL. Greenhouse conditions are probably favourable for mass-release of parasites as they enable an extensive growth of plants and rearing of host aphids. However, there are several factors that seem to restrict their favourability to certain periods of the season. Greenhouses cannot be practically isolated as quarantine rooms can be, so that accidental invasion of out-of-doors species is very probable; it may either include the accidental introduction of other insects that attack the plants grown, or other parasites, predators, or hyperparasites. These agents can cause considerable trouble in a mass-production program. Nevertheless, it is obvious that the probability of such accidental introductions is restricted to the period when these insects occur in nature, i.e. during the vegetation season. In winter, and in early spring or late autumn in a temperate zone, there is no such danger. Thus, heated greenhouses are best used in a mass-rearing program during the period from late autumn up to early spring; even during spring, if the invaders are accidentally introduced, they do not seem to be so important as they do not succeed in reproducing so much up to the period when the mass-reared material is planned to be released (during the spring period).

Another trouble, which restricts the use of greenhouses for certain periods of the season, is the control of temperature conditions. In winter, there is no doubt that

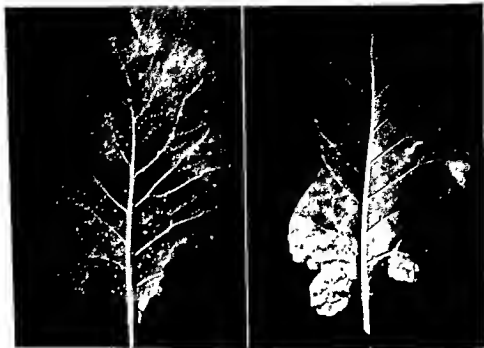


Fig. 321. Biological control in greenhouses. Experimental program. Czechoslovakia. Left: Brassica-leaf heavily infested by *Brevicoryne brassicae* and *Myzus persicae*, parasite: *Diaeretiella rapae*. Right: Brassica-leaf heavily infested by *Myzus persicae*, parasite: *Diaeretiella rapae*.

control of temperature and photoperiod does not cause any trouble; artificial light sources and controlled photoperiod are sometimes necessary because of the regulation of the aphid life-cycle. However, during the hot summer months, it is much more difficult to cool larger greenhouses to such temperatures that would not be fatal to many aphids and parasites reared.

If parasites are reared perennially in a greenhouse, their accidental or purposeful escape may follow and they establish themselves in the greenhouse neighbourhood. However, it depends on the species and on its requirements on the environment whether this establishment is successful or not: a species may be well adapted to survive given climatic conditions, but lack of the host may prevent its establishment outside the greenhouse in a given area. Or, some populations or strains of parasites may not be capable of surviving outside the greenhouse, although a favourable host may occur in there; the latter is obviously the case of the Californian greenhouse strain of *Aphidius matricariae* (see SCHLINGER & MACKAUER, 1963).

According to our preliminary investigations, unheated or so called summer greenhouses if placed on certain plots of the field, may cause earlier growth of plants and development of a pest population. introduced parasites may be added to such greenhouses and may develop favourably there, later in spring, the greenhouse is removed and the parasite population may spread over the field. Especially plastic material serving as a cover for these summer greenhouses could be useful and cheap. We have applied this method in the mass-release of introduced parasites of alfalfa aphids in Czechoslovakia, but experiments on a wider scale are necessary (see: Biological control program).

The above mentioned method of application of summer greenhouses could be also applied with respect to the action of indigenous parasites, as our preliminary experiments on alfalfa fields have shown; the conditions in a summer greenhouse inhibit—due to a higher temperature that occurs in the greenhouse—the development of the fauna, both of aphid and parasite populations, when compared with field conditions. If the parasites are present in the field and successfully overwinter, they can reproduce more rapidly and reach a higher population density; after the removal of the greenhouse cover significant sources of parasite population might develop that would attack the pest aphid much earlier than would occur in nature (see: Biological control program).

REFERENCES. 31, 166, 301, 414, 421, 440, 450, 637, 705-8, 761, 794, 831, 1006, 1069, 1102, 1214, 1234, 1319.

COUNTRIES. This review represents brief information on the biological control of aphids by parasites in separate countries of the world. Detailed records on aphids and parasites may be found in aphid and parasite reviews.

— ARGENTINE. Biological control of *Schizaphis graminum* through releases of the indigenous parasite, *Lysaphidius platensis*, was undertaken by GRIOT. Rfcs.: Griot 1944, 1949, Millan 1956.

— AUSTRALIA (and Tasmania). A number of undetermined parasites were introduced into Australia from various countries at about the beginning of this century. Most of the releases were unsuccessful (see: review of parasites). The controlled objects were *Toxoptera aurantii*, *Brevicoryne brassicae*, and undetermined aphids.

Tuberculoides annulatus: *Praon flavinode* and *Trioxys pallidus* were introduced to Tasmania from England, where the parasites became established and controlled the aphid. They accidentally spread into Australia.

Caviariella aegopodii has become an object of biological control in recent years. *Aphidius salicis* was introduced from California to control the pest (STUBBS). Rfcs.: DeBach 1962, 1964, Jenkins 1948, Miller 1947, Miller et Hudson 1953, Stubbs 1966, Wilson 1960.

— CANADA. Biological control of aphids in greenhouses was dealt with by BAIRD (1935) and MCLEOD (1937, 1939): *Myzus persicae* was the main object of the control.

In recent years, experiments with *Aphidius smithi* have been undertaken to control *Acyrtosiphon pisum* on alfalfa (MACKAUER & BISDEE 1965). Rfcs.: Baird 1935, Mackauer et Bisdee 1965, McLeod 1937, 1939).

— CUBA. Aphid fauna with respect to biological control was dealt with and the projects on the introduction of parasites elaborated. No practical control activities were undertaken. Rfcs.: Starý 1967, 1968.

— CZECHOSLOVAKIA. *Megoura viciae* was the object of experiments on biological control. *Aphidius megourae* population was introduced (intraareal introduction) (STARÝ 1964).

Hyalopterus pruni has been dealt with, *Aphidius transcaspicus* was introduced (STARÝ 1964, 1965, 1966).

Acyrtosiphon pisum is another object of control experiments. Besides the research on the conservation of indigenous parasites, experiments on the introduction of *Aphidius smithi* have been undertaken (STARÝ 1966). Otherwise, various projects on parasite conservation were elaborated. Rfcs.: Starý 1959, 1964, 1965, 1966.

— FRANCE. *Brevicoryne brassicae* has become a project of biological control by an indigenous parasite, *Diacretiella rapae*. Rfcs.: Broussal 1962, 1966.

— GERMANY. Proposals on conservation of *Diacretiella rapae* populations in certain

periods of the year were elaborated on the basis of seasonal history studies (SEDLAG 1964). Possibilities to use *Lysiphlebus fabarum* for the control of *Myzus persicae* and *Aphis fabae* are dealt with (Biol. Control Inf. Bull. 1967). Rfcs.: Biol. Control Inf. Bulletin 1967, Sedlag 1964.

— GREAT BRITAIN. ARTHUR (1945) made experiments on the control of cereal aphids by inoculation of native parasite populations. *Aphidius matricariae* was used in control of *Myzus persicae* in greenhouses (Biol. Control Inf. Bull. 1967). Rfcs.: Arthur 1945, Biol. Control Inf. Bulletin 1967.

— INDIA. Survey of natural enemies of a number of pest aphids is reported (*Myzus persicae*, *Aphis gossypii*, *Acyrtosiphon pisum*, *Lipaphis pseudobrassicae*, *Brevicoryne brassicae*, *Aphis spiraeicola*). Rfcs.: Biol. Control Inf. Bulletin 1967.

— ITALY. Some proposals on parasite conservation in Citrus and peach orchards were elaborated. Rfcs.: Starý 1964, 1965.

— MEXICO. *Therioaphis trifolii*, an introduced pest, was an object of biological control by introduced parasites, *Praon exoletum* and *Trioxys complanatus*. Rfcs.: Padilla et Young 1959.

— NEW ZEALAND. Biological control projects dealing with aphids on cereals and crucifers are reported. Rfcs.: Biol. Control Inf. Bulletin 1967.

— PAKISTAN. Research of aphid parasites with respect to their potential use in biological control is reported. Rfcs.: Biol. Control Inf. Bulletin 1967.

— POLAND. *Aphidius smithi* was experimentally introduced to control *Acyrtosiphon pisum*. Rfcs.: Wiackowski et Wiackowska 1961.

— PERU. *Aphis gossypii* was an object of biological control (? by parasites). Rfcs.: Huangui et Combe 1956.

— URUGUAY. Artificial release of the indigenous parasite, *Lysaphidus platensis*, was made to control *Schizaphis graminum*. Rfcs.: Silveira Guido et Conde Jahn 1946, Millan 1956.

— USA. Several unidentified species were introduced into Hawaii from various countries at the beginning of this century. There are no recoveries mentioned. In 1923 *Lysiphlebus testaceipes* was introduced and successfully established to control various aphids; another population of the parasite was introduced in 1965 to control *Aphis nerii*. *Acyrtosiphon pisum* became an object of biological control in 1960 when the introduced *Aphidius smithi* was released and successfully established. Rfcs.: Annual report 1960-61, 1961-2, 1963, 1965, Beardsley 1961, Bianchi 1941, Davis 1961, Davis et Krauss 1962, DeBach 1964, Fullaway 1915, 1923, 1924, 1932, Holdaway et Nishida 1946, Illingworth 1929, Imms 1924, Krauss 1962, Notes and exhibitions 1924, 1928, 1929, 1931, 1946, Pemberton 1948, Swezey 1925, 1929, 1931, 1935, 1937, Swezey et Bryan 1929, Timberlake 1927, Williams 1931.

In California, *Therioaphis trifolii* was the first aphid to which biological control through utilization of introduced parasites was applied (*Trioxys complanatus*, *Praon exoletum*). Many research workers have dealt with this problem, starting with the search for a parasite abroad, release and establishment, up to the detailed post-introduction studies both in the laboratory and field. The intensity of the work was stimulated by the great economic significance of the introduced pest and it has stimulated the research of parasites in many other countries.

Acyrtosiphon pisum, another pest on alfalfa, has been controlled by the introduced *Aphidius smithi*. Numerous studies on the further development of host-parasite population relations were undertaken.

Aphis fabae, *Trioxys angelicae* and *Lysiphlebus* sp. were introduced from Lebanon (1967).

Chromaphis juglandicola, a pest aphid on walnut, has also become an object of

biological control. There was a parasite, *Trioxys pallidus*, introduced and established in California.

Hyalopteris pruni. *Aphidius transcaspicus* is reported to be introduced from Lebanon to California (1967).

Rhopalosiphum nymphaeae. *Aphidius transcaspicus* is reported to be introduced from Lebanon to California (1967).

Citrus pest aphids are reported to be controlled by experimentally introduced parasites. Rfcs.: Anonymus 1961, Biological Control Inf. Bulletin 1967, v. d. Bosch 1956, 1957, v. d. Bosch et al. 1959, 1962, 1964, 1966, Clausen 1956, DeBach 1962, 1964, Finney et al. 1960, Fisher et al. 1959, Hagen et al. 1958, Hagen et Schlinger 1960, Schlinger 1960, Schlinger et Hall 1960, Schlinger et Mackauer 1963, Sluss 1967, Sluss et Hagen 1966, Smith R. F. 1959, Starý et Schlinger 1967, Stern et v. d. Bosch 1959, Wiackowski 1960, 1961, etc.

In other continental States, experiments on the biological control of *Macrosiphum rosae* by utilization of native parasites were undertaken by WITHINGTON (1909) in Kansas (greenhouses).

Indigenous parasites were also utilized in the control of *Schizaphis graminum* in Kansas: *Lysiphlebus testaceipes* populations were translocated from the south to western parts of the State (HUNTER 1909, HUNTER & GLENN 1909, WEBSTER 1909).

Therioaphis trifolii has become an object in a number of States because of its spread in the Nearctic America; the biological control activities were undertaken on the basis and in connection with the successful biological control of the aphid in California.

Acyrtosiphon pisum has been also subject to control in many western and eastern States, where *Aphidius smithi* was introduced to control the aphid.

Experiments on biological control of potato aphids were undertaken in the eastern States (Maine) as part of a complex research program (SHANDS et al. 1965).

Rfcs.: Angalet et Coles 1960, Barnes 1960, Clausen 1956, 1958, Cooke 1963, Dowden 1957, Hunter 1909, Hunter et Glenn 1909, Nielson et Barnes 1961, Shands et al. 1965, Webster 1904, Withington 1909.

During recent years, aphid parasites have become a source of accepted agents in biological control of aphids. Basic research has been started and continued in many countries and interest in the group has been paid in a number of institutes over the world.

HABITATS AND CROPS. It is very instructive to mention briefly the separate kinds of habitats as well as the crops with respect to biological control of aphids by parasites; only introduced parasites are dealt with. Abbreviations: established (+), no records or research in progress(?), unsuccessful (—).

Annual crops. Brassica: *Brevicoryne brassicae* (+); Phoeniculum: *Caravelia aegopodii* (+?); Solanum tuberosum: *Myzus persicae* (?); Vicia faba: *Megoura viciae* (—; no satisfactory program).

Perennials. Medicago sativa (alfalfa): *Acyrtosiphon pisum* (+); *Therioaphis trifolii* (+).

Deciduous orchards. Prunus domestica: *Hyalopteris pruni* (?); Prunus persica: *Hyalopteris pruni* (?); Juglans regia: *Chromaphis juglandicola* (+).

Evergreen orchards. Citrus spp.: *Aphis gossypii*, *Aphis spiraeicola*, *Toxoptera aurantii* (all?).

Ornamentals. Nerium oleander: *Aphis nerii* (?).

Deciduous forest. Quercus (introduced): *Tuberculoides annulatus* (+).

(Note: The general occurrence of *Lysiphlebus testaceipes* as a parasite of various aphids in Hawaii is not mentioned; see: biological control in islands).

There are various opinions as to whether the biological control is more perspective on annual or on perennial crops. In our opinion it seems more useful to classify the ecosystems in accordance with their stability; such a classification is more instructive than the separation of crops into annual and perennial ones. We have shown that the perennial character of a community does not simultaneously mean that the given ecosystem is stable with respect to aphid parasites, as the aphids may decrease this stability basically by migration; this is obvious, for example, in problems of *Hyalopterus pruni* control in temperate orchards, control of Citrus pest aphids, etc. There is no doubt that at least relatively stable communities are obviously the best for biological control attempts.

APHIDS - CONTROL OBJECTS. There are a number of records on the natural limitation of aphids by parasites. However, the review of biological control records is surprising in how little has been relatively achieved in the application of parasites. Although the number of records is rather high as there are many records on introduced parasites whose hosts to be controlled were unknown, the situation seems to be rather stimulative. There are many different pest aphid species all over the world, in which biological control has not yet been applied (parasite action).

- *Acyrtosiphon pisum*. U.S.A.-California: *Aphidius smithi* (V. D. BOSCH & SCHLINGER 1965, V. D. BOSCH et al. 1966, DEBACH 1964, HAGEN & SCHLINGER 1960, SCHLINGER 1960, SCHLINGER & HALL 1960, SMITH & HAGEN 1966, WIACKOWSKI 1960, 1962).

U.S.A.-Western States: *Aphidius ervi* (COOKE 1963). *Praon pequodorum* and *Aphidius pulcher* (COOKE 1963). *Aphidius smithi* (COOKE 1963).

U.S.A.-Eastern States: *Aphidius smithi* (ANGALEY & COLES 1966).

U.S.A.-Hawaii: *Aphidius smithi* (Annual Report 1960-61, 1961-62, 1963, BEARDSLEY 1961, DAVIS 1961, DAVIS & KRAUS 1962).

Canada: *Aphidius smithi* (MACRAUER & BIRDIE 1965).

Poland: *Aphidius smithi* (WIACKOWSKI & WIACKOWSKA 1961).

Czechoslovakia: *Aphidius smithi* (STARÝ 1966).

- *Aphis craccivora*. U.S.A.-Hawaii: *Lysiphlebus testaceipes* (see: islands).

- *Aphis fabae*. Germany: *Lysiphlebus fabarum* U.S.A.-California: *Trioxys angelicae*, *Lysiphlebus* sp.

- *Aphis gossypii*. U.S.A.-Hawaii: *Lysiphlebus testaceipes* (see: islands). U.S.A.-California: (V. D. BOSCH 1961, STARÝ & SCHLINGER 1967).

PETU: (HUANGUI & COMBE 1956).

- *Aphis nerii*. U.S.A.-Hawaii: *Lysiphlebus testaceipes* (Annual Report 1965).

- *Aphis spiraeicola*. U.S.A.-California: (V. D. BOSCH 1961, STARÝ & SCHLINGER 1967).

- *Aulacorthum solani*. U.S.A.-Maine: *Aphidius* sp., *Aphidius smithi* (SHANDS et al. 1965).

- *Brericonyia brassicae*. Australia: (DEBACH 1964, JENKINS 1948, WILSON 1960).

- *Cavariella oenopodii*. Australia: *Aphidius salicis* (STUBBS 1966).

- *Chromaphis juglandicola*. U.S.A.-California: *Trioxys pallidus* (DEBACH 1962, 1964, SCHLINGER 1960, SCHLINGER et al. 1960, SLUSS 1967, SLUSS & HAGEN 1966).

- *Hyalopterus pruni*. Czechoslovakia: *Aphidius transcaspicus* (STARÝ 1964, 1965, 1966).

U.S.A.-California: *Aphidius transcaspicus* (Biol. Control Inf. Bull. 1967).

- *Longunguis sacchari*. U.S.A.-Hawaii (PEMBERTON 1948, DEBACH 1962, 1964).

- *Macrosiphum euphorbiae*. U.S.A.-Maine: *Aphidius* sp., *Aphidius smithi* (SHANDS et al. 1965).

- *Macrosiphum rosae*. U.S.A.-Eastern States: *Ephedrus unicompletus* (WILKINSON 1969).

- *Megoura viciae*. Czechoslovakia: *Aphidius megourae* (STARÝ 1964, 1966).
- *Myzus persicae*. Canada: *Aphidius matricariae*, *Ephedrus persicae* (BAIRD 1935, MCLEOD 1937, SMITH 1931).
- Germany: *Lysiphlebus fabarum* (Biol. Control Inf. Bulletin 1967).
- Gr. Britain: *Aphidius matricariae* (Biol. Control Inf. Bulletin 1967).
- U.S.A.-California: (v. D. BOSCH 1961).
- U.S.A.-Maine: *Aphidius matricariae* (SHANDS et al. 1965).
- *Rhopalosiphum nymphaeae*. U.S.A.-California: *Aphidius transcasicus* (Biol. Control Inf. Bulletin 1967).
- *Rhopalosiphum maidis*. U.S.A.-Hawaii: *Lysiphlebus testaceipes* (see: islands).
- U.S.A.-California: *Ephedrus persicae* (Biol. Control Inf. Bulletin 1967).
- *Schizaphis graminum*. U.S.A.-Kansas: *Lysiphlebus testaceipes* (HUNTER 1909, HUNTER & GLINN 1909, WEBSTER 1909).
- Argentina: *Lysaphidus platensis* (GRIOT 1944, 1949, LOPEZ CRISTOBAL 1937, MILLAN 1956).
- Uruguay: *Lysaphidus platensis* (SILVEIRA GUIDO & CONDE JAHN 1937).
- *Sitobium* sp. Great Britain: *Aphidius avenae* (ARTHUR 1944, 1945).
- *Therioaphis trifolii*. U.S.A.-California: *Praon exoletum*, *Trioxys complanatus* (Anonymus 1961, v. D. BOSCH 1956, 1957, v. D. BOSCH et al. 1959, v. D. BOSCH & SCHLINGER 1962, 1964, DEBACH 1962, 1964, FINNEY et al. 1960, HAGEN et al. 1958, SCHLINGER 1960, SCHLINGER & HAGEN 1965, 1966, STERN 1962, 1966, STERN & v. D. BOSCH 1959, WIACKOWSKI 1960).
- U.S.A.-Arizona: *Praon exoletum*, *Trioxys complanatus* (BARNES 1960).
- U.S.A.-Utah: *Praon exoletum*, *Trioxys complanatus* (GOODARZY & DAVIS 1958, KNOWLTON 1966).
- Mexico: *Praon exoletum*, *Trioxys complanatus* (PADILLA & YOUNG 1959).
- *Tinocallis caryacfoliae*. U.S.A.-California: *Trioxys pallidus* (SCHLINGER et al. 1960).
- *Toxoptera aurantii*. U.S.A.-Hawaii: *Lysiphlebus testaceipes* (see: islands).
- Australia: (WILSON 1960).
- U.S.A.-California: (v. D. BOSCH 1961).
- *Tuberculoides annulatus*. Australia (Tasmania): *Trioxys pallidus*, *Praon flavinode* (DEBACH 1962, Ent. Problems 1940, MILLER 1947, WILSON 1960).

PARASITES - CONTROL AGENTS. Originally, we intended to elaborate a review of world species of the Aphidiidae that would include the main information as to their distribution, habitat, host list, host range, and the main literary records on their biology, in order to give the applied workers a source of brief information on the separate species. However, in the meantime, there has appeared the idea of O.I.L.B. workers to publish the Index of Entomophagous Insects, the main task being to revise and summarize our recent state of knowledge of the various groups; naturally, besides the taxonomic role, this Index is intended as a basic source of information for the applied workers. As the Aphididae, elaborated by MACKAUER & STARÝ (1967), were included in the second volume of the Index, we have decided to avoid duplicity and leave our original idea; instead, we present below a brief review of all the aphid species that were used as agents in a biological control of aphids. It is obvious from this list that we are just at the beginning of the introduction practice in the aphidiids. There are undoubtedly many possibilities of using some of the species in aphid control.

During our biological control work, we have elaborated several projects of pest

aphid control (citrus, cocoa, coffee, sugar cane, banana), where a number of parasite species were selected to be dealt with in applied research. However, these projects were not included in this review as no practical work has yet been undertaken (STARÝ 1966, 1967).

- *Aphidius asenae*. This parasite, as an indigenous species, was introduced in cereal fields to control corn aphids in England. The development of the introduced populations was observed and compared with the normal dispersal and further development of parasite populations in other fields (ARTHUR 1944, 1945).

- *Aphidius ervi*. Populations of this species were introduced from France and Germany into the western United States in 1963 for control of *Acyrtosiphon pisum* (COOKE 1963).

Populations from Eritrea and Lebanon were introduced to California in 1962 for control of *Acyrtosiphon pisum* (MACKAUER & STARÝ 1967).

- *Aphidius matricariae*. This species was used in biological control of *Myzus persicae* in greenhouses in Canada. Populations were collected in the field and transferred to the greenhouse, where they were successfully cultured and proved to be an excellent control in the warmest greenhouses; sprays were not necessary in consequence (BAIRD 1935). It was also found effective in greenhouse conditions by MCLEOD (1937) and SMITIT (1931). The use of this species in aphid control in greenhouses is also reported from Great Britain (Biol. Control Inf. Bulletin 1967).

Populations were introduced from France to Maine in 1957, 1958 to control potato aphids. Recovery low, no substantial increase (SHANDS et al. 1965).

Populations from Iran and Israel were introduced to California in 1960. Mass rearing and release in California (MACKAUER & SCHLINGER 1963).

- *Aphidius megourae*. Populations from the environs of Moscow, U.S.S.R., bred from *Megoura viciae*, were introduced into Czechoslovakia in 1962, reared in the laboratory and initially established in 1963 (intra-areal introduction). No recoveries were made in subsequent years due apparently to the release of material in low numbers on annual crops (*Vicia faba*), time of release (autumn), and heavy infestation of predatory thrombiculid mites in the natural release plot. The control object was *Megoura viciae*. The experiments were principally intended to serve as a certain course in laboratory research on parasite biology as well as development of methods used in the field, the techniques being later applied in parasites of true pest aphids.

Rfs.: Starý 1964, 1966.

- *Aphidius pulcher*. Populations of this species were transferred from New Jersey to western U.S.A. to control *Acyrtosiphon pisum*. Initial establishment and permanent establishment were successful (COOKE 1963).

- *Aphidius salicis*. Populations introduced from California to Australia. Release in 1962. In 1963 further recovery and successful release. Now widely distributed in Melbourne and adjacent areas (STUBBS 1962). Note: according to unpublished information of R. D. HUGHES these populations belong to at least two species neither of which is the original introduction from California.

Rfcs.: Mackauer et Starý 1967, Stubbs 1966

- *Aphidius smithi*. The original populations were collected and reared from *Acyrtosiphon pisum* on alfalfa in India. Laboratory stock reared at New Delhi. 110 aphid mummies sent to Moorestown, U.S.A., insectary, the material provided 17 ♀♀ for use in propagation work. During 1958 and 1959 more than 74,000 were produced. Object of control: *Acyrtosiphon pisum*.

Released: western United States: Washington, Oregon, Idaho, California, Utah, Colorado, Arizona. eastern United States: Delaware, New Jersey, Philadelphia, Vancouver, Nova Scotia. The stock was sent to California insectaries (see: below).

In 1961, releases (from Californian stock) in Oregon and New Jersey. Recoveries: subsequent to the release in 1958 recovered in Delaware, New Jersey; every following year attempts were made to recover the species at various release sites but results were negative. In the autumn of 1965, however, recoveries were from several localities in New Jersey, Pennsylvania, and Delaware, parasitization 18% (max. 25%) in collections taken. In November 1965 recovered in North Carolina and Maryland. The observations made in 1965 show that the parasite is established and suggested that it might become a widely dispersed and important parasite in the eastern United States (ANGALET & COLES 1966).

In Maine, introduced and released in 1958 to control potato aphids. No recoveries (SHANDS et al. 1965). This failure in establishment is obviously due to propagation of the parasite on other hosts in the field. As far as it is known, it attacks *Acyrtosiphon pisum* only.

In California, releases were started in alfalfa fields in 1958 and by May 1960 more than 220,000 parasites were released. The parasite became established in several coastal valley alfalfa fields in 1958 and by the following spring the colonics were spreading rapidly into surrounding fields. In the autumn of 1959 the parasite was exerting considerable control of the aphid in most colonized coastal valleys. A survey in spring 1960 showed that the parasite became widespread in many anterior valleys, including the desert regions of southern California. The absence of the aphid in the inland valleys during the summer does not enable the parasite to survive in sufficient numbers to become permanently established; there is no aestival quiescence in the parasite to survive such a period. Other factors limiting the effectiveness are absence of alternative hosts, adverse weather conditions, and harvesting practices. Considerable research has been prolonged. The success is substantial.

Rfcs.: v.d. Bosch 1965, 1966, v.d. Bosch et Schlunger 1965, v. d. Bosch et al. 1966, Cooke 1963, DeBach 1964, Finney et Fisher 1964, Hagen et Schlunger 1960, Mac-kauer et Bisdee 1965, Stern et al. 1964, Wiackowski 1960, 1962.

Introduction to Hawaii: insectary stock population sent from California. Introduced on November 3rd and 10th, 1960. Release number and periods: November 1960 - 750, January 1961 - 655, February 1961 - 200, March 1961 - 2000; 3,605 altogether. Host: *Acyrtosiphon pisum* on alfalfa. Recovery a month later after release at Ewa, Oahu. It has since been liberated and recovered in Kauai and Maui. Field collections showed heavy parasitization. Recoveries also in 1963. Success spectacular (F. J. SIMMONDS, unpublished suggestion).

Rfcs.: Annual Report 1960-61, 1961-62, 1963, Beardsley 1961, Davis 1961, Davis et Krauss 1962.

Introduction to Czechoslovakia: first laboratory stock received from Riverside, California in 1962; only laboratory studies were undertaken and the relationship of the introduced species to the indigenous *Aphidius ervi* was dealt with, the parasite being incorrectly supposed to be identical. Host: *Acyrtosiphon pisum*. Another shipment obtained from Albany, California in 1967. Laboratory studies, mass-rearing and release experiments are in progress.

Introduction to Poland: populations were introduced from Riverside, California into Poland in 1960. Laboratory studies undertaken, release made on alfalfa fields. Host: *Acyrtosiphon pisum*. No further records.

Rfcs.: Wiackowski 1960, Wiackowski et Wiackowska 1961.

Introduction to Canada: in 1964 laboratory stock was sent from California to Belleville, Canada, and reared in the quarantine laboratory. In the same year, the parasite was taken in the commercial alfalfa fields, being fairly abundant. As the species had been liberated in various localities of the eastern United States as early as

1958, an immigration via the Niagara Peninsula or across the Upper St. Lawrence River seemed more likely. It is still a question, whether the parasite is actually established in southern Ontario or merely invades this part of the country annually from the eastern United States (MACKAUER & BISDEE 1965). The authors seem to overestimate the role of the (accidentally) spread introduced parasite on Canadian alfalfa fields studied. It is mentioned as having displaced a native parasite species, although it is obvious from the tables mentioned in their paper that the native parasites were rare or even lacking at the localities where the introduced parasite was not established.

Rfes.: Mackauer et Bisdee 1965.

- *Aphidius transcaspicus*. Populations were received from Italy and Israel 1964 (H. pruni). Releases made in 1964, 1965 and 1967 in Czechoslovakia. Initial establishment successful. The research on the factors that influence the permanent establishment is still in progress.

The parasite is also reported to be introduced from Lebanon to California and used in biological control of *Hyalopterus pruni* and *Rhopalosiphum nymphaeae* (Biol. Control Inf. Bulletin 1967).

Rfes.: Biol. Control Inf. Bulletin 1967, Starý 1964, 1965, 1966.

- *Aphidius* sp. Populations were introduced from France in 1962 to Maine to control potato aphids. Release period and release number mentioned as favourable, small chance of establishment (SUANDS et al. 1965).

- *Aphidius* sp. Population of this species was introduced from Japan in 1913 into the Hawaiian islands to control an unknown aphid species. Failure of establishment (SWEZEY 1931).

- *Diaeretiella rapae*. This species is reported as having been introduced into Hawaii in 1902 (WILSON 1960).

- *Ephedrus incompletus*. Indigenous populations of this species were found effective in controlling *Macrosiphum rosae* in greenhouses in the eastern United States (WITHERINGTON 1909).

- *Ephedrus persicae*. Indigenous populations of this species were used in control of *Myzus persicae* in greenhouses in Canada (MCLEOD 1937).

Populations were introduced from Lebanon to California in 1965 (MACKAUER & STARÝ 1967) to control *Rhopalosiphum maidis* (Biol. Control Inf. Bull. 1967).

- *Ephedrus plagiator*. Populations were introduced from Taiwan into California in 1961. Additional releases were from Japan to California in 1965 (FLESCIENER 1963, MACKAUER & STARÝ 1967).

- *Lysiphidius platensis*. Native populations were artificially inoculated in cereal fields to control *Schizaphis graminum* in Argentina and Uruguay (GRIOT 1944, SILVEIRA GUIDO & CONDE JAHN 1946, MILLAN 1956).

Populations were introduced from Brazil to California (MACKAUER & STARÝ 1967).

- *Lysiphidius fabarum*. Populations were introduced from Lebanon to California in 1965 (MACKAUER & STARÝ 1967). It is reported to be used in control of *Myzus persicae* and *Aphis fabae* in Germany (indigenous populations) (Biol. Control Inf. Bull. 1967).

- *Lysiphidius testaceipes*. Intra-areal introduction in Kansas. Indigenous populations were used in artificial inoculation on cereal fields attacked by *Schizaphis graminum* in northern areas. The delay of parasite occurrence that occurs in natural coincidence was believed to be overwhelmed in this way. Artificial foci developed, 20-30,000 parasitized aphids put in each, considerable reduction of aphid number in consequence reported (HUNTER 1909, HUNTER & GLENN 1909). WEBSTER (1909) reports that experimental distribution of the parasites for control of the aphid gave negative

results. Some records mentioned need a revision: one ♀ is reported to have killed as many as 2,000 aphids during 25 days and 10,000 aphids during 30 days (!).

Introduction to Hawaii (1): populations were introduced from California to Hawaii in 1923. Release and recovery successful (see: islands) (ILLINGWORTH 1929, Notes and exhibitions 1924, 1928, 1929, 1931, 1946, SWEZEY 1931, 1935, 1937, SWEZEY & BRYAN 1929, WILLIAMS 1931).

Introduction to Poland: populations were introduced from California to Poland (laboratory) in 1960 (WIACKOWSKI & WIACKOWSKA 1961).

Introduction to Hawaii (2): another population of parasites was introduced from Mexico to Hawaii in May 1965, to control *Aphis nerii*, which immigrated to Hawaii in February, 1965 (Ann. Report 1965). First, it is a question whether *Aphis nerii* had to be controlled. We have found it to be an important alternative host of *Lysiphlebus testaceipes* in Cuba, where its significance as alternative host of this parasite seems to be greater than the damage which is made by the aphid to Nerium shrubs. Further, it is not apparent whether an earlier introduced population (1923) of the parasite would not also attack the aphid.

Introduction to Czechoslovakia: populations were introduced from Cuba to Czechoslovakia in 1966. In a heated greenhouse they were successfully reared for several months on *Aphis spiraeicola* and *Toxoptera auranti* on Citrus, and on *Rhopalosiphum maidis* on maize. Later they did not survive as their hosts died due to unfavourable conditions of their host plants. No field releases were made.

Rfcs.: Annual report 1965, Beardsley 1961, Bianchi 1941, Fullaway 1915, 1924, 1932, Holdaway et Nishida 1946, Hunter 1909, Hunter et Glenn 1909, Illingworth 1929, Notes and exhibitions 1924, 1929, 1929, 1931, Swezey 1931, 1937, Swezey et Bryan 1929, Webster 1909, Wiackowski et Wiackowska 1961, Williams 1931.

– *Lysiphlebus* sp. Populations were introduced from Japan to Hawaii in 1913. Failed to become established (SWEZEY 1931).

– *Lysiphlebus* sp. A species is reported to be introduced from Lebanon to California to control *Aphis fabae* (Biol. Control Inf. Bull. 1967).

– *Praon exoleum*. Populations were introduced from Mediterranean region and the Middle East into California in 1955–56 and became widely distributed over the state as well as in other states during the years. Control of the host, *Therioaphis trifolii*, considerable. Released in other states (Utah, Arizona, Mexico) or naturally spread. Extensive information may be found in the literature. The parasite, similarly to *Trioxys complanatus*, may be classified as the first parasite applied in the biological control of an aphid pest in accordance with a well elaborated program.

Rfcs.: Anonymus 1961, Barnes 1960, Bartlett 1958, v.d. Bosch 1956, 1957, v. d. Bosch et al. 1964, DeBach 1964, Finney et al. 1960, Goodarzy et Davis 1958, Hagen et al. 1958, Harpaz 1955, Knowlton 1966, Luti 1961, Nielson et Barnes 1961, Padilla et Young 1959, Schlenger et Hall 1960, Smith R. F. et Hagen 1965, Stern et v. d. Bosch 1959, Stern et al. 1958, Wiackowski 1960.

– *Praon flavinode*. Populations were introduced in 1936–8 from England to Australia to control *Tuberculoides annulatus* (WILSON 1960).

– *Praon pequodorum*. Populations were introduced from New Jersey to control *Acyrtosiphon pisum* in eastern Washington and Oregon (COOKE 1963).

– *Praon volucre*. Populations were introduced from Europe to the U.S.A. (MACKAUER 1959).

Populations were introduced from Israel to California in 1960 (FLESCHNER 1960).

Note: WILSON (1960) reports this species as being introduced from England to Australia, however, this is apparently *Praon flavinode* as *P. volucre* does not attack the aphid mentioned.

- *Trioxys angelicae*. Populations were introduced from Israel to California in 1960 (FLESCIENER 1963).

Populations were introduced from Lebanon to California in 1965-6 (MACKAUER & STARÝ 1967) to control *Aphis fabae*. (Biol. Control Inf. Bull. 1967).

- *Trioxys communis*. Populations were introduced from Taiwan and released in California in 1961 (FLESCIENER 1963).

- *Trioxys complanatus*. Similarly as *Praon exoletum*, the species was introduced from the Mediterranean and Middle East to California in 1955-6 to control *Therioaphis trifolii*. It has become widespread over the state during the years as well as in some other states. In some states it was purposely released, while naturally spreading to others. Considerable information may be found in the literature.

Rfcs.: Anonymous 1961, Barnes 1960, Bartlett 1958, v. d. Bosch 1956, 1957, v. d. Bosch et al. 1964, Conrad et Medler 1965, DeBach 1964, Finney et al. 1960, Goodarzy et Davis 1958, Hagen et al. 1958, Knowlton 1966, Liuti 1961, Nielson et Barnes 1961, Padilla et Young 1959, Schlinger et Hall 1960, Smith R. F. et Hagen 1965, Stern et v. d. Bosch 1959, Wiackowski 1960.

- *Trioxys pallidus*. Introduction to California: populations to control *Chromaphis juglandicola* were introduced from France in the late spring of 1959. Initial field colonization in 1959 (and continued to 1962). Successfully established, highly effective in some districts, principally because of close coincidence with the host's occurrence (v. d. BOSCH et al. 1962). In northern California released in 1961 and 1962, recovery in 1964; the parasite successfully overwintered; parasitization in samples 1963-23%, 1964-only 9% (SLUSS 1967); it does not seem to play an important role in the population dynamics of the aphid (SLUSS & HAGEN 1962).

Another population was introduced from Iran to California in 1960. The stocks of the Iranian population are expected to survive better in the warmer walnut areas in California than the French population (v. d. BOSCH et al. 1962).

Rfcs.: v. d. Bosch et al. 1962, DeBach 1962, 1964, Fisher et al. 1959, Schlinger 1960, Schlinger et al. 1960, Sluss 1967, Sluss et Hagen 1966.

Introduction to Tasmania (as "*Trioxys aceris* Haliday"): Populations were introduced in 1936-8 from England to Australia to control *Tuberculoidea annulatus*. Established in 1939. No further introductions, but the parasite became distributed in Tasmania during 1939-1941; as a result of the natural and artificial spread of the parasites the aphid became heavily parasitized in many areas of Tasmania. The parasite was accidentally introduced to Australia.

Rfcs.: Ent. problems 1940, Evans 1939, Muller 1947, Wilson 1960.

- *Trioxys* sp. Populations were introduced from California to Hawaii in 1907 to control *Toxoptera aurantii*. No further data available (SWEZEY 1931).

- *Unidentified parasite species*. Origin various, mentioned in a complex of natural enemies. Introduced into Hawaii in 1900-1923 to control *Longiniquis sarchari* (DEBACH 1964, PEMBERTON 1948).

From: Queensland and N.S. Wales. Introduced: other parts of Australia. Host: *Brevicoryne brassicae*. Release 1902. No further data. WILSON (1960) correctly mentioned that this is probably *Diaretella rapae*, which is commonly distributed both in western and eastern Australia, being first recorded from Australia in 1902 (ALEXANDER 1925, WILSON 1960).

From: N.S. Wales. Introduced: Queensland. Host: aphids. Release: 1902 (WILSON 1960).

From: Queensland. Introduced: western Australia. Host: aphids. Release: 1902 (WILSON 1960).

From: Marseille, France. Introduced: western Australia. Host: *Toxoptera aurantii*. Release: 1903 (WILSON 1960).

From: Seville, Spain. Introduced: western Australia. Host: aphids. Release: 1903 (WILSON 1960).

From: Algeria. Introduced: western Australia. Host: *Toxoptera aurantii*. Release: 1906 (JENKINS 1946, WILSON 1960).

From: Ceylon. Introduced: western Australia. Host: *Toxoptera aurantii*. Release: 1907 and 1909 (JENKINS 1946, WILSON 1960).

From: Colombo, Ceylon. Introduced: Australia. Host: *Brevicoryne brassicae*. Release: 1907 (WILSON 1960).

From: Ceylon. Introduced: Australia. Host: *Brevicoryne brassicae*. Release: 1907 (partial results) (DEBACH 1964, JENKINS 1948, WILSON 1960).

From: Orient. Introduced: Australia. Host: *Brevicoryne brassicae*. Release: 1909 (WILSON 1960).

APHID-VECTORS. According to MARAMOROSCH (1963) the types of aphid transmission of plant viruses can be characterized by two extremes:

1. Non-persistent or mechanical, in which aphids can acquire and transmit a virus within a matter of seconds or minutes, but soon lose the ability unless they have access to another virus source.

2. Persistent or non-mechanical, where aphids often require hours for transmission, but where they continue to transmit virus for many days after removal from the virus source. However, there is a great number of intermediates, which are neither persistent nor non-persistent.

With respect to the circulation in the aphid body, there are stylet-borne or circulative viruses distinguished. In stylet-borne viruses the infectivity is lost when the aphid moults, in circulative viruses the virus is ingested and passes to the salivary glands and in this case the infectivity is not lost when moulting (KENNEDY, DAY & EASTOP 1962).

Virus transmission by aphids can vary in three ways: (1) variation in virus transmission among different clones or strains of one species, (2) variation among developmental stages, (3) variation among different forms of one species (MARAMOROSCH 1963).

It is obvious from the comparison of the types of virus transmission by aphids and the influence of parasitization on the host that the parasites are not capable of preventing the transmission of the disease if the aphid-vector attacked the plant: on the one hand, viruses are mostly transmitted by alate aphids, while most of the parasites prefer low instar aphids when ovipositing and mummify them prior to the aphids reaching maturity. On the other hand, even the parasitized aphids have enough time to transfer the virus as the parasite larval development needs several days for completion and the larva kills the aphid, and this time is more than sufficient for the transmission of the virus by the vector.

Thus, it seems that the parasites can only reduce the population of potential vectors inside the crops or in stands from which the aphids disperse. However, also in this case the aphid number that survives seems to be sufficient for dissemination of the disease. The parasites, contrary to predators, do not lower the aphid density in a colony to low levels which would be too low for alate production (comp. BONNE-MAISON 1948) as the parasitized aphids mostly remain inside the colony. In every case, there is no doubt that a low population density of aphids-vectors is enough to cause injury, while such a density of aphids causing injury by sucking could be negligible (see: STERN et al. 1959). This point of view may also change the relative

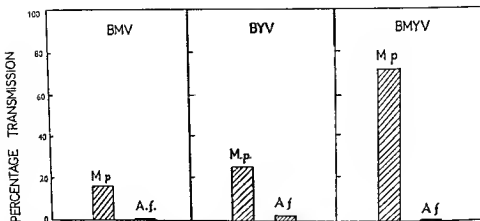


Fig. 322. Infestivity of alatae after developing and flying from sugar beet plants infested with viruses. Each result is based on the number of transmissions by 40-150 aphids tested singly, in pairs in groups of three (COCKBAIN & HEATHCOTE 1965). *M.p.* - *Myzus persicae*, *A.f.* - *Aphis fabae*, BMV - beet mosaic virus, BYV - beet yellow virus, BMVY - beet mild yellowing virus.

significance of parasites in control of different aphid species attacking the same crop. For example, according to COCKBAIN & HEATHCOTE (1965) there is no doubt that *Myzus persicae* is a more important pest, although less numerous in the sugar beet stands, than *Aphis fabae*, on sugar beet. With respect to parasites, we could then expect that even a high percentage of parasites of *A. fabae* would be less significant with respect to the injury than the relatively lower parasitization of *M. persicae* (Fig. 322). Consequently, the parasites seem to be only partially helpful in vector control.

Our above mentioned opinion is not based on experiments, but only on the evaluation of parasite effectiveness both if the parasites act as limitation or control agents, where 100% parasitization of host population is rare and may be observed only in some colonies. It is necessary to add this, as BARTLETT & V. D. BOSCH (1964) expressed a contrary opinion, however, with respect to general biological control problems, where natural enemies are mentioned as being capable of maintaining their hosts at exceedingly low densities.

AUTOCIDAL CONTROL. Autocidal control has been experimentally dealt with also in aphids. Various substances have been proved in order to recognize the possibility of using certain agents in aphid control, for example, of chemosterilants. As this method has been found to be useful when applied to certain insects, there is a theoretical possibility that it could be found also useful in aphid control programs. For this reason, we should deal here, at least preliminarily, with the application of autocidal control methods in aphid pest control and its possible significance for the parasites.

The aphids are mostly parthenogenetic, in any case during a certain part of the season. This phenomenon seems to eliminate a sterile male method. However, when the progeny of the parthenogenetic aphids would be affected in a certain way, then it is a question whether the chemical agents would be selective in action or whether they would influence the parasite larva that develops within the parasitized aphid. When the agent would be selective, the aphid would gradually produce progeny of an inferior quality, there would be no influence on the parasite. When the agent

would not be selective, the autocidal aphid control would represent simultaneous elimination of parasite population; in this case, the parasite could survive only when attacking other aphid species. These preliminary considerations as well as the problem of ecological homologues and community equilibrium with respect to autocidal control of aphids are a matter for future research.

Rfcs.: Bhalla et Robinson 1966, Harries et Wiles 1966.

REFERENCES. 6, 10, 11, 12-3, 23, 30, 32, 34, 45, 52, 56, 63, 67, 81, 85, 99, 104, 106, 113-7, 121-32, 155, 158, 166, 172, 176, 180, 200, 201, 204, 206, 208-11, 217, 235, 243, 245-6, 247-8, 252-5, 258, 259, 260, 261, 268, 270, 275, 276, 280, 281, 290, 291, 295, 301, 319, 347, 354, 355, 360-1, 362, 366, 368, 371, 380, 382, 386, 392, 394, 395, 402, 403, 417-9, 421-5, 470, 473, 476, 478, 497, 499, 502, 503, 506, 508, 511, 515, 547-9, 557, 561, 563, 597, 599, 623, 632, 635, 647, 648, 664, 674, 688, 689, 702, 736, 749, 751-4, 756-7, 762, 767, 771, 772, 774, 787, 805, 806, 816, 860, 882, 884, 896, 897, 899, 909, 946, 951-3, 955, 957, 965, 969, 992, 1001, 1002-5, 1014, 1017, 1020-2, 1023, 1026, 1030, 1035, 1039-40, 1048, 1051-3, 1055-61, 1064, 1065, 1069, 1071, 1072, 1074, 1075, 1079-80, 1081, 1092, 1098, 1103, 1121, 1122, 1123, 1125, 1130, 1133, 1151, 1154, 1157, 1158, 1190, 1196, 1199, 1202, 1229, 1236, 1250, 1266, 1270, 1279, 1284, 1295, 1299, 1300, 1307, 1315.

Integrated Control of Aphids

PRINCIPLES AND TERMINOLOGY. Integrated control has been defined as the integration of cultural, chemical and/or physical control methods with the effect of enemies of pests (FRANZ 1961, fig. 323).

The basic principles of integrated control have been summarized by SMITH (1962, 1963) as follows:

1. The complete complex of organisms, the culture of the crop and the conditioning environment are considered together as a unit—the ecosystem.
2. The population levels at which pest species cause harm, or damage or are a nuisance, must be determined and control measures directed to keep pests below these economic levels rather than attempt to eliminate them completely.
3. Necessary control measures should be designed to give adequate control but in a manner which does not upset some other part of the ecosystem.

There are some difficulties as to the delimitation of the ecosystem. Integrated control measures are developed around a certain crop and thus the given crop area should limit the ecosystem. Nevertheless, as mentioned by SMITH (1962), some wide-ranging organisms, such as aphid species (*Therioaphis*, *Toxoptera*), make delimitation of the ecosystem extremely difficult. We have perhaps solved the matter in elaborating the multilateral control concept (Chapter XIII), which basically supports the integrated control around a certain crop, but the neighbouring ecosystems whose members may invade and influence the given controlled ecosystem are also dealt with. A multilateral control concept stresses the avoidance of a research of an ecosystem, which should be controlled without any basic information on the other ecosystems in which the sources of the key pests may occur. Multilateral control was originally elaborated on aphids and their parasites, as the aphids represent just pest organisms which alternate either obligatorily or facultatively the various ecosystems in the course of the season.

The integrated control approach has been elaborated purposely to prevent as much economic loss due to pest occurrence as possible. This approach means that not all the insect species which occur in the given ecosystem are of equal value. Our main interest is naturally paid to the consumers of the plants, i.e. the phytophagous insects. Consequently, SMITH (1962) divided the pest species into three groups:

The first group includes persistent pests, which cause harm practically throughout the whole season.

The second group represents the occasional pests, which cause economic losses only in certain years, where the environmental conditions allow their numbers to reach economic levels.

The third group includes the potential pests, which do not cause significant damage under current conditions.

It is a very important feature of integrated control that the key pest species should

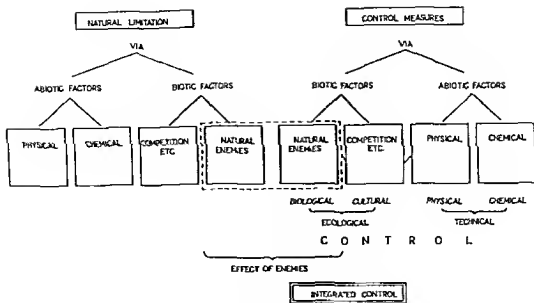


Fig. 323. A scheme of natural limitation and control relation (after FRANZ, 1961).

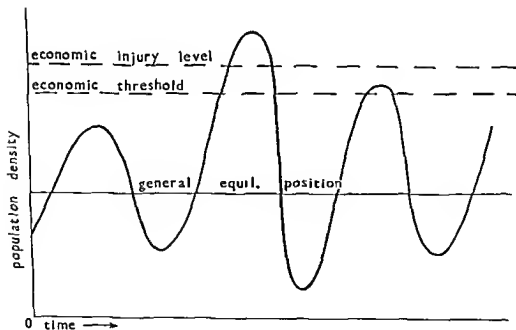


Fig. 324. Schematic graph of a theoretical arthropod population over a period of time and its general equilibrium position, economic injury level and economic threshold (STERN, 1966).

be handled in a very careful manner so as not to upset the natural limitation or control of the occasional or potential pests (see: SMITH, 1962).

The next basic point and problem of integrated control is the determination of population levels at which a given organism is considered to be a pest. It has been mentioned in the natural limitation chapter that the population of every species which occurs in a given ecosystem has a certain equilibrium position, around which its population number fluctuates. This is a natural state which occurs in all the ecosystems. Nevertheless, the interests of man should avoid some fluctuations in pest population levels, as on these levels the pest causes considerable damage to the crop, the agroecosystems are just characterized by far less stability than the natural ecosystems. STERN et al. (1959) have developed the classification of pest population levels for integrated control purposes as follows: apart from the general equilibrium position which is a natural state, they distinguish the economic injury level, which is the lowest pest population density that will cause economic damage. As the integrated control measures need a certain period before they come into action with respect to the population controlled, it is necessary to distinguish another population level at which the control measures must be applied to prevent the pest population reaching economic injury level. Such a population level was classified as an economic threshold by the mentioned authors (Fig. 324). Thus, before an integrated control program is developed, we must know the general equilibrium position, the economic threshold and the economic injury level at least in the key pest species. It must be mentioned as an addition that the economic threshold is not a constant phenomenon; it varies depending on the crop, season, area and desire of man.

Another rather important phenomenon of integrated control may be derived from the above classification of pest population density levels. Integrated control does not require the eradication of a pest population in a given ecosystem. The levels of the pest population beneath the economic levels must be preserved because of the stability of the ecosystem, as a certain pest population density is necessary for the occurrence of the natural enemies of the pest in the given ecosystem. The elimination of the pest species would influence the community stability and cause a possible adverse situation as is known in numerous cases of insecticide applications which were carried out irrespective of ecosystems.

APHIDS AS CONTROL OBJECTS. Some basic features of aphids as a group with respect to integrated control should be mentioned.

Aphids occur practically in all types of terrestrial habitats of the world. The monoculture character of the agroecosystems is very suitable for them.

As to the number of species, the aphids are distributed mostly in a temperate zone, in the subtropics and to a small degree in the tropics. However, even in the tropics they are rather significant pests, although the distribution of many pest species is due to agriculture.

The aphids represent pests of all the above mentioned kinds, i.e. permanent, occasional and potential pests. They are also known to be typical potential pests which become significant due to non-selective insecticide treatment.

The aphids alternate the ecosystems during their life, thus being either an obligatory or facultative phenomenon. This enables them to invade an ecosystem, namely the crop cultures and to reach high levels before the natural enemies are able to influence their numbers.

Aphids exhibit a rather powerful reproductive potential and they are capable of reaching economic levels in a very short time when environmental conditions are favourable.

Due to their numbers and occurrence of alate progeny they are able to spread and disperse rather rapidly.

The aphids may occur perennially on a certain crop or they may be only seasonal pests.

Aphid species in a given crop may occur in a succession, some species occurring only in a certain crop (apple, *Dysaphis plantaginea*, *Aphis pomi* in the temperate zone of Europe, etc.). Or the species may occur perennially, but the peak numbers of separate species are reached in a succession (alfalfa, *Acyrtosiphon pisum* and *Therioaphis trifolii* in Europe, California, etc.).

Variability of the economic threshold as well as of economic injury levels is rather different in the same or different aphid species. The same aphid species may cause different kinds of damage on different crops. It may be of less value on a perennial crop and important on the annuals. It can cause damage by sucking on one crop and be a significant vector on another crop. It may be a pest on irrigated lands and remain beneath economic levels on non-irrigated lands, etc. Further, the level of economic damage is gradually lower as we try to obtain as much harvest as possible.

On the other hand, aphids are attacked by a number of natural enemies, which are considerably important in influencing the population numbers of the aphids.

APHID PARASITES AS AGENTS. In the classification of natural enemies with respect to integrated control SMITH (1962) divided them into the three following groups, which naturally also cover the aphid parasites:

1. The first group includes the so called incidental natural enemies, which are of little or no importance in host population determination and are in fact merely dependent on their hosts as a source of energy.

Many aphidiid parasites could be mentioned. They are either generally rare species, which are connected with the ecosystem, or they may be species which are rare in the given ecosystem but which may be common and effective in other ecosystems due to their occurrence as parasites of more preferred hosts, habitat and microhabitat preference, etc. Nevertheless, with respect to the given ecosystem their role in limiting the population numbers of a given pest is the same.

2. The second group includes the natural enemies which are partially effective in pest population determination. They may reduce a pest population to subeconomic levels in some years, in some places, or in certain seasons, or they contribute to a lowered general level of the pest. These natural enemies are very important in integrated control programs.

It seems that the greatest part of the aphidiid parasites, which attack the economic pests, belong to this group and thus their significance is well documented. The aphidiids are a part of the aphid natural enemy complex and consequently their effectiveness seems to be generally partial in the course of the season.

The parasites take part also in determining the pest population in other ecosystems and thus also in this respect the multilateral control approach must be stressed.

This aspect on the aphidiid parasites seems to change basically their classification with respect to their use in aphid control. In earlier times, when "full" biological control was requested, the aphidiid parasites often were not considered to be very useful. For example, ULLYETT (1938), who dealt with the influence of *Diaeretiella rapae* on the populations of *Brevicoryne brassicae* in S. Africa, was rather sceptical as to parasite effectiveness, presuming that it is clear that, generally, the parasite labours under serious disadvantages (interspecific competition with predators, action of hyperparasites, sex ratio, climate) which are apparently insurmountable. We could re-classify such an opinion from the integrated control point of view in that inter-

specific relations, hyperparasites, sex ratio and climate are the common factors which influence the population number of every natural enemy in a given ecosystem. Nevertheless, if the given parasite (natural enemy) exhibits a partial effect in limitation or control of its host population in a given ecosystem, it might be valuable and useful in an integrated control program, as its action, as well as the action of other species of a similar character, can be supported and completed by other control measures.

3. The third group includes the completely effective natural enemies. These species keep the potential pests below economic threshold all, or at least, most of the time.

In the aphids, because of their position in the complex of natural enemies, such effectiveness seems to be rare. Perhaps, only the spectacular cases of biological control such as *Acyrtosiphon pisum* - *Aphidius smithi* in Hawaii could be mentioned; in this case, however, both the host and parasite are introduced organisms as well as the host plant, the alfalfa, so that the conditions of the ecosystem, the alfalfa field, exhibit peculiar (oceanic island) features.

IDEAL STATE AND REALITY. The ideal way to develop an integrated control program was summarized by BEIRNE (1961). This way means, (1) to introduce as many biotic agents into the picture as possible; then, (2) to intensify their effects by suitable environmental manipulations; (3), to apply appropriate insecticides to suppress incipient outbreaks where necessary.

It is obvious that a really complete integrated control program, or the optimum integrated control program as mentioned by BEIRNE, needs a quantity of records on each pest species in a given ecosystem. And we must stress that these ecosystems differ from each other in separate countries, even though the plant community, i.e. the crop, may be the same. Thus, if we bear in mind this fact, the number of research teams, the financial costs, the organization of practical attempts, the education of both administrative agencies as well as the farmers, there is no doubt that the reality differs considerably from the ideal state. Nevertheless, this state must not be discouraging. We should keep in our minds also the whole story of insect pest control and all the trends, the successes achieved and the mistakes made. There is no doubt that an integrated control approach is the only trend for the present and the future control of pests. Undoubtedly different levels in various countries and on various crops and a wide range of modifications will exist, but the principal trend will remain the same. Furthermore, the really scientific approach to the problem and elaboration of the foundations of integrated control is a matter of a little more than 10 years and even during this relatively short period significant results were achieved in various countries of the world, especially in the U.S.A. in California.

ERADICATION AND INTEGRATED CONTROL. It is well known that eradication has many positive features and it has been successfully applied on several insect objects. Eradication measures may be relatively short-termed, the development of resistant insects is less probable, eradication technique may be specific for one species and, finally, the environment is not contaminated (DEBACH 1964).

However, eradication is a complicated problem, just as to its relation to integrated control of pests.

The first viewpoint is that of the object, the aphid pest. It seems that the aphids do not represent a suitable object for eradication. The reproduction is parthenogenetic for the greatest part of the season and thus excludes the application of the sterile male method. Further, the aphids spread and disperse rather widely due to the common occurrence of their alate forms, so that the recolonization of the plot by other popu-

lations can soon be expected. Finally, the aphids are attacked by a number of natural enemies in nature, the activity of which should be exploited in the interest of man.

The second viewpoint is that of the ecosystem. The application of insecticides shows that if a population of one species is eliminated in a given ecosystem, the population of another species that was little or not at all touched by the treatment may increase to economic levels. In the agricultural crops especially we could expect a similar situation in the case of the eradication of an aphid population. Then, the occurrence of natural enemies, including parasites, would be made impossible because of the eradication of their food source, the aphids.

The third point of view is the duration of the eradication effect in a given ecosystem. We have shown above that invasion of other aphid populations into a given plot can soon be expected. This considerably decreases the value of eradication as a method of aphid control, as the pest can appear again, while the natural enemies, including parasites, are absent. This situation closely resembles that which occurs due to insecticidal treatment. We can only agree with SMITH & REYNOLDS (1966) that eradication is the antithesis to integrated control, just because an integrated control program often requires the continuous existence of a pest population (low densities, subeconomic levels) in the given ecosystem.

DEBACH, when dealing with the relation of pest population eradication and the action of parasites, mentioned a possibility that natural enemies should be imported and established as a preliminary to eradication procedures directed against well established pest species; it is well known that the lower the pest population density is to begin with, the earlier and more economical it is to secure eradication by the use of sterile ♂♂ or other techniques, etc. In our opinion this could be useful in an eradication program of vectors of diseases of human health, etc., but as (aphid) pests of agriculture in continental areas the integrated control seems to be preferable owing to the above mentioned reasons.

Program

ECOSYSTEM. As we have shown in the natural limitation chapter the ecosystems exhibit a various degree of stability. The classification of the given ecosystem with respect to its stability is of basic significance in the integrated control program. Annual crops are generally mentioned to be rather unstable ecosystems due to their short growing season, which does not provide sufficient time for the development of an equilibrium between the host and natural enemy populations. There is no doubt that annual crops are practically restricted to a period of one year or even one season at a given place, when they are drastically influenced by cultural practices and similar ecosystems associated with the given crop start to develop in the course of the next year. Nevertheless, even in annual crops we recognize different degrees of stability, the period of harvest being perhaps the most significant. The cut flower plantings are probably least stable, while annual crops are harvested at the end of the growing season and exhibit considerably greater stability. Integrated control of aphids in annual crops on peppers (SHOREY 1961, 1962, etc.) has shown that even in annual crops this program could be successful. The ecosystems of a semi-permanent or permanent character such as perennial crop fields, orchards, and forests appear to be more suited to the development of an integrated control program. Naturally, even there, there could be difficulties such as a great number of key pest species, etc. In the permanent communities such as forests, which have a long rotation period when compared with crops, the basic difficulty is in determining the economic level of the separate forest pests (see: SMITH 1963, FRANZ 1966).

PEST APHIDS. The kind of injury caused to the given crop is important as the control measures considerably change when an aphid is controlled as a sucking pest or as a vector. Seasonal history of the aphid and its relation to the given ecosystem is the next feature: an aphid may be a seasonal or perennial inhabitant in a given ecosystem and this has an influence on the natural limitation and control measures. For example, if the aphid is a perennial inhabitant in a relatively stable ecosystem, we can expect that its population increase will soon be followed by the increase of the parasite (natural enemy) population, and then selective insecticide application to reduce the aphid population below the economic threshold can be expected to be favourable for the action of the parasites. On the other hand, if we have an annual crop and the aphid first immigrates to the crop field, we can expect a rather poor limitation of its numbers during a considerably long period before the parasites are able to disperse over the field and in this case it seems that aphids could be controlled much below economic levels without danger of negatively affecting the increase of parasite population levels. The relation of the crop field to the neighbouring ecosystems, especially to those where the sources of the pest aphid occur, should be dealt with. The next step in pest classification is the determination of economic levels. It depends widely on the type of injury and kind of plant. When these economic levels are determined, the effectiveness of parasites (natural enemies) to limit aphid numbers is evaluated in order to recognize in which parts of the season we can expect them to be helpful and in which parts of the season some gaps in aphid limitation by parasites are probable. The reason of outbreak, whether it was due to climatic and plant conditions, or whether it was caused by a treatment directed to another pest, should be determined.

CONTROL MEASURES. We have dealt with biological control in a separate chapter and thus its role in integrated control is only briefly mentioned here.

Biological control, as one of the parts of integrated control, consists generally of augmentation and conservation of indigenous parasites, and of the introduction of parasites from abroad and their further augmentation and conservation. There is no doubt that some of the means to conserve the parasites can be undertaken only by integration of the control methods, but this does not mean that biological control should be identical with integrated control. Although we are aware of such opinions, they seem to be unjustified in diminishing the significance of purposefully used bionic agents in the integrated control. From this point of view, we must again support the definition of integrated control as mentioned by FRANZ (1961). There is a natural state which is called natural limitation. We can partially influence this state in a purposeful way through using biological, physical, chemical and cultural measures. Biological control must be considered as a means which is equivalent each to the other one mentioned.

— **CULTURAL CONTROL.** 1. *Orchard undergrowth. Cover crops and clean cultivation.* Although orchards exhibit a number of forest features due to a relatively long rotation period, they have many unnatural features. Of these features the problem of undergrowth is rather significant. There is no doubt that generally a rather heterogeneous plant cover such as orchard undergrowth is rather important for improving a greater heterogeneity of the orchard ecosystem. From this point of view, a clean cultivation system seems to be of questionable value. The introduction of suitable cover crops, which enrich the soil by important nutrient substances, seems to be a progressive trend, although research is needed as to whether this system is favourable enough as (1) the plant heterogeneity may be low to allow many parasitic

insects to find adult food and alternative hosts there, and, (2) even in a cover crop system the orchard undergrowth is cultivated.

The aphid parasites exhibit somewhat different biological features that make them different from the other entomophagous insects, nevertheless, we must not forget that the whole ecosystem must be dealt with; for example, if even rich undergrowth is not useful for the aphidiids, it may be a favourable environment for other natural enemies of aphids and other entomophagous species.

The problem of undergrowth with respect to aphid parasites is widely dependent on the composition of the aphid pests which attack the fruit trees and, to a lesser degree, on the climatic zone.

In most cases, the fruit tree pest aphids are attacked by the parasites associated with deciduous forest habitats and this means that they do not parasitize the aphids living in the undergrowth but search only for aphids which occur in the tree- and shrub-layer. On the contrary, the aphid species in the undergrowth are attacked mostly by a number of species associated with steppe habitats. Thus, in the temperate zone at least, the parasite complexes associated with fruit trees and undergrowth are two different groups; naturally, some intermediate cases are also known, but they are relatively rare. Therefore, first, with respect to parasites of fruit tree pest aphids, the shrubs and other trees in the orchard or orchard undergrowth are more important as a source of alternative hosts than the undergrowth, secondly, the undergrowth of a heterogeneous type might serve as a chronic focus of parasites of various field crop aphid pests.

Nevertheless, there is another problem, that of clean cultivation. It is known that many of the aphidiids overwinter inside mummified aphids which are attached to fallen leaves. Clean cultivation, which means the covering of these cocoons by a layer of soil, is fatal to the cocoons. The influence of this layer on the parasite emergence was well documented experimentally (see: WAY 1965, HOZÁK in press). Thus, even if the heterogeneity of the undergrowth would not be important with respect to aphid parasites, the clean cultivation system is fatal to overwintering parasite cocoons.

A somewhat different situation as to the relation between undergrowth and tree-layer may be found in the subtropics and the tropics, where the habitat-dependence of parasites exhibits somewhat different features than in the temperate zone. We have shown in the chapter on parasite foci that the pest species or alternative hosts of the parasites can commonly be found both in the tree and undergrowth layer in the orchards (Cuba). From this point of view, the undergrowth has a direct relation to the limitation or control of fruit tree pest aphid, in the tropics (*Aphis spiraeicola*, *A. craccivora*, *A. gossypii*, etc., in Cuba). The significance of shrubs and other trees in an orchard neighbourhood is the same as in a temperate zone.

2. Shade trees, way-side trees and various ornamental shrubs and trees are rather important for parasite conservation, for example in the environment of orchards. We have shown in the chapter on parasite foci that they may be a source of both pest aphids and/or alternative hosts of the parasites. Consequently, such plant species should be preferred which are the host plants of economically indifferent host aphids that are attacked by parasites which attack also economic pests. For example, *Nerium oleander* can be mentioned. It is attacked in many countries by a relatively narrowly specialized *Aphis nerii*, which attacks other ornamentals or meadow plants, but does not attack economic crops. This aphid is attacked commonly by *Lysiphlebus ambiguus* in S. Europe and this parasite attacks a number of pest aphids such as *Toxoptera aurantii* on Citrus, *Aphis punicae* on *Punica granatum*, etc. Similarly, in Cuba, *Aphis nerii* is attacked by *Lysiphlebus testaceipes*, which is a parasite of *Toxoptera aurantii*, *Aphis spiraeicola*, *A. craccivora*, *A. gossypii*, *Rhopalosiphum maidis* and other pest aphids.

Thus, the possible significance of *Nerium oleander* plants in parasite conservation is well documented.

3. Pruning and fertilizing in orchards. There is a great difference between a growing praxis in old and modern orchards. This state was well summarized by WILDBOLZ (1965): apple trees in a modern orchard differ fundamentally from those of former times. The period of growth was confined to spring in such sparingly fertilized standard trees, and ceased soon after their flowering. Growth similar to that in young trees is now maintained until late summer by pruning and fertilizing. This modern system of apple growing is connected with the amount of vegetative growth and just these young suckers are the favourite food for many aphids and consequently the aphids have become more significant pests in apple orchards. This state in modern orchards has been well documented by several authors (BODENHEIMER & SWIRSKI 1957, POST 1962, WILDBOLZ 1965).

The occurrence of many aphid species in orchards will thus be longer, due to the modern growing system. This means on the one hand, there could be a greater possibility of host-parasite population balance to develop, nevertheless, there is another problem of parasite population density and the degree of aphid limitation by parasites in such orchards.

4. Weeds. We have dealt with the weed problem in the chapter on parasite foci. In connection with integrated control we should have only to mention that the aphid fauna and associated parasites must be evaluated, in order to recognize whether the weeds and associated fauna have a certain possible useful relation to the neighbouring crops or not, whether they are a source of pest aphids, etc. In many cases, weeds may be useful in providing greater plant heterogeneity and stability of the ecosystem.

5. Uncultivated lands have common features in exhibiting great heterogeneity in plant cover and associated fauna. There may be some larger or smaller places where the original virgin community survived the general cultivation of the virgin landscape, or there may be secondarily uncultivated plots, which are often covered by many weed plants; commonly, too, there occurs a mixed community, composed of members of virgin communities and weed plants, etc.

These uncultivated lands, besides their incidental role in providing a supply of parasites (and sometimes even pest aphids) to the neighbouring crop fields, might be purposefully used as places for growing many honeyplants, both herbs and shrubs. This has a positive role in apiculture (TOMŠIK *et al.* 1953) and possibly it could have a positive role also in parasite conservation (see: STARÝ 1962, 1964, 1966 *etc.*).

6. Intercropping is a purposeful growing of narrow strips of crops along larger plots of other crops with the intention of providing a greater heterogeneity of plant cover. As both the crops may be associated with a different fauna and there may be a different succession, the interrelations among the members of the faunas might be useful in natural enemy conservation and pest limitation.

The intercropping program was, for example, proposed by SHANDS *et al.* (1965) in the potato districts of Maine, but only predators were dealt with. When a similar program would be dealt with in parasites, careful examination of host of separate parasites that occur in such systems would be necessary and the relationship of the parasites to pest aphids attacking both the crops should be made only on this basis. For example, in Europe, alfalfa, sugar beet and potato fields have almost no interrelations as to aphid parasites.

7. Strip farming constitutes a state when various crops are planted in strips. This strip farming means improvement of greater plant heterogeneity in the agricultural landscape. As to the nomenclature, we have therefore followed MARCOVITCH (1935)

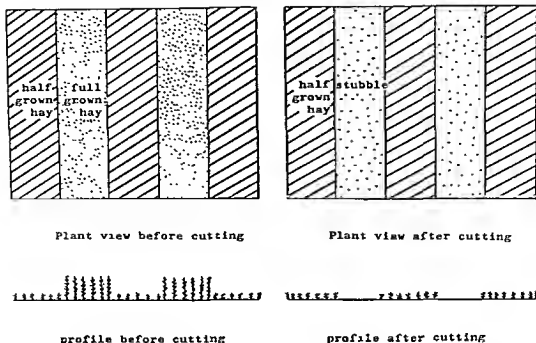


Fig. 325. Diagram of cutting procedure used in strip harvested fields in California. Strips were 120 feet and 150 feet wide, resp. in the two fields studied in 1963 (STERN, V.D. BOSCH & LEIGH 1964).

who developed this program on an experimental basis, when studying the relations of the fauna associated with turnips, beans, peas, corn, cowpeas, cotton, okra, cucumbers and water melons.

As is obvious, strip farming is closely related to intercropping and exhibits similar problems as to the aphid parasites.

We should mention that we do not consider the alfalfa strip cutting or strip harvesting programs as developed by Californian authors (SCHLINGER & DIETRICK 1960, etc.) to be a strip farming program, although it was classified in this way by V. D. BOSCH & TELFORD (1964). According to our opinion the expression "strip farming" should be preserved for the farming of different crops (see the above classification).

8. A strip cutting program has been developed by Californian authors (SCHLINGER & DIETRICK 1960, STERN, V. D. BOSCH & LEIGH 1964, V. D. BOSCH et al. 1964, V. D. BOSCH & TELFORD 1964, V. D. BOSCH et al. 1966 etc.) as a practice which protects, at least partially, the community stability of the alfalfa field. Generally, it is a modified harvesting program allowing parasite conservation and favourable host-parasite population relationship to be undisturbed.

In principle, strip cutting is a process of cutting and harvesting hay from alternate strips in the same field. When each set of alternate strips of hay matures and is cut, the other strips are about one-half grown. Thus, strips of growing hay are always available for the pest species as well as the natural enemies, and a more satisfactory population balance between each pest and its natural enemies can be maintained during the entire growing season (V. D. BOSCH & TELFORD 1964) (Fig. 325).

The Californian authors found that the generally used system of a single cutting of the whole field is rather unfavourable to parasite survival and to host-parasite population relations. The single harvest system means the removal of parasite mummies and even many aphids (green chopping), the parasite and host adults

Natural enemies	Average number per acre		
	Regular farming	Strip farming	Increase
Lady beetles adults	46,000	205,000	159,000
Lady beetles larvae	11,000	232,000	221,000
Green lacewing larvae	195,000	206,000	11,000
Parasitic wasps	70,000	287,000	217,000
Big-eyed bugs	199,000	401,000	202,000
Predatory spiders	105,000	1,094,000	989,000
Totals	626,000	2,435,000	1,809,000
Total per sq. ft.	14	56	42

Table 16. Strip-cutting alfalfa program. Important natural enemies of *Therioaphis trifolii*, Brawley, 1959 (SCHLINGER & DIETRICK, 1960).

emigrate, and both populations must again re-invade the field. Experimental evidence comparing the results obtained in normally mown fields and strip-cut fields clearly showed the positive features of the strip-cutting system in alfalfa fields. This system was useful both in *Therioaphis trifolii* and *Acyrtosiphon pisum* integrated control programs. In *Th. trifolii*, there were 70,000 parasites found per acre of alfalfa in regular farming, while there were 287,000 in strip farming plots. A similar state was found in *A. pisum* (Table 16).

The strip cutting program is useful both when the hay is taken in green chopping or in baling systems. In every case, the alternate strips of half-grown or fully grown alfalfa allow a quick re-establishment of host-parasite population relations in the cut and gradually newly grown strips.

It seems that the strip cutting program will be of use not only in cases of introduced parasites, but also in cases of indigenous parasites of alfalfa pest aphids (C. Europe).

CHEMICAL CONTROL. There are numerous opinions as to the use of pesticides, their positive and negative roles. The situation was briefly summarized by STERN et al. (1959). According to these authors the following problems have appeared with the use of insecticides:

1. Arthropod resistance to insecticides. Many aphid pests in various parts of the world are known that are capable of developing resistant strains to the separate insecticides used. The chemical control of the resistant aphid strains necessitates other kinds of insecticides being used, there being further complications as to the influence of these insecticides on the ecosystem.

2. Secondary outbreaks of arthropods other than those against which control was originally directed. Aphids may be considered to be typical pests of this kind. Numerous cases are known when aphid outbreaks followed the application of insecticide against another pest.

3. The rapid resurgence of treated species necessitating repetitious insecticide applications. Aphids are capable of re-invading the treated plot and reaching further outbreaks in a very short time owing to their ability to disperse through alate progeny.

4. Toxic insecticide residues on food and forage crop.

5. Hazards to insecticide handlers and to persons, livestock, and wildlife subjected to contamination by drift.

6. Legal complication from legal suits and other actions pertaining to the above problems.

Economic levels of pest aphids are one of the factors that influence the degree of insecticide application in a given ecosystem.

In a great number of cases the aphids cause injury to their host plants by sucking and weakening of plants followed by the appearance of various deformations, etc. In this case, the aphid levels are relatively high even before they reach economic threshold levels when insecticidal application follows to re-establish the favourable relation of host-natural enemy populations. Thus, in such cases, the aphid populations must occur in a given community to allow the occurrence and action of natural enemies.

Nevertheless, many aphids cause injury to the crops by transmission of virus diseases and in such cases their economic levels are extremely low, obviously much lower than those on which the natural enemies (parasites) are able to keep them. Better to say, the aphids are just important before the host-natural enemy population relations may develop (annual crops namely). It seems that the proper insecticidal application may be the only means of preventing or controlling the aphid-vector population, while the natural enemies (parasites) will be perhaps, at least partially, helpful in reducing the pest aphid populations in untreated places (other ecosystems). – *Selectivity of insecticides.* Selectivity of an insecticide is the measure of the capacity of treatment to conserve natural enemies while destroying pests (BARTLETT 1964).

According to BARTLETT and other authors, selectivity may be divided into the two following groups:

Physical selectivity originates from differential exposure of pests and natural enemies to the pesticide. Physical selectivity may be classified according to different points of view.

1. Selectivity derived from the preservation of natural enemy reservoirs outside the treated area.

In general, natural enemy reservoirs or the foci as we call them can be preserved outside the field of a given crop, or inside the field through modification of the treatment program.

In the first case, treatment is applied in the whole field, while the reservoirs of parasites (natural enemies) in the field neighbourhood are not touched and the parasites may gradually disperse from there and re-invade the field. This situation requires the neighbourhood of a crop field which would include foci of parasites in which the population density of parasites would be high enough to allow parasite dispersal. Alternative hosts of parasites could be useful. Nevertheless, there is another possibility, that there would occur in the neighbourhood of the crop field reservoirs of the pest and parasites so that the problem of re-invasion could be dealt with from this point of view too. The mentioned situation does not occur in extensive areas of monoculture crops which are typical for many intensively cultivated districts.

In the second case, the reservoirs of natural enemies (parasites) are preserved in the crop field so that the occurrence of natural enemies in a given area does not depend on the field neighbourhood. This may be reached by spot treatment or strip treatment practices.

2. Selectivity derived from a different susceptibility of developmental stages of natural enemies.

As is mentioned below, the parasites exhibit a rather different susceptibility to pesticides in separate developmental stages, namely in accordance with their dependence on the host.

3. Selectivity derived from distinctive feeding habits of natural enemies.

In aphid parasites, we can generally differentiate three kinds of feeding habits with respect to the influence of insecticides. The first kind of feeding habit is connected with

the parasitic life and adult stage to about the last instar larva stage, which occurs in the living aphid. The second kind does not practically mean a kind of feeding as the parasites during these periods do not feed at all, and they are protected from external influences by the cocoon. This period covers a part of the last instar larva stage, the prepupal stage, the pupal stage, and the pre-emergence period of the adult stage. The third kind is the feeding of parasite adults, which do not feed on the host but on its honeydew. These three kinds of feeding habits influence the sensibility of the parasites to an insecticide rather significantly and it is not possible to select a perfectly selective insecticide which would leave all the parasite stages untouched as some of them are attached to a living host whose population is at least partially killed by the treatment. Thus, in praxis, the selectivity of an insecticide with respect to parasites will be restricted only to parasite stages which are not dependent on the living hosts (mummified aphids, adults).

4. Selectivity derived from distinctive seasonal life-histories and habitats of natural enemies.

As we have shown in various chapters (seasonal history) the requirements of aphids and parasites exhibit specific features and this, in connection with the peculiarities in aphid biology and conditions of the environment, may cause the temporary separation of host and parasite populations. The cultural crop fields, annual crops most of all, represent a typical case which allows the aphids to occur temporarily in an environment where they are not attacked by natural enemies. During this period the insecticidal treatment can considerably reduce the immigrating aphid population numbers which could soon reach an economic threshold, but the natural enemies (parasites) are not affected (sugar beet, potatoes etc.). The microhabitat also plays a significant role. Insecticides of a certain mode of action may not reach a certain part of the aphid population in certain shelters or on less exposed parts of the plants and this part of the population consequently survives the treatment. If the parasites prefer such shelters, a higher percentage of parasitization will occur in these shelters which escape the action of insecticides. Generally, the insecticides of systemic or fumigant action considerably reduce this possibility (for example see: SHOREY 1961).

5. Selectivity derived from distinctive physical features of pesticides and their application.

These features are of two kinds. The first one is the dosage of insecticides. It is well known that dosage reduction plays an important role in favouring the natural enemies, while higher dosages of the same insecticide are fatal. Numerous examples could be mentioned (see: STERN et al. 1959, etc.).

The second feature is the toxic residue of the given insecticide. It is closely related to the question of dosage. Toxic residue may influence the newly emerged parasite adults which were protected from the influence of insecticide inside the mummified aphids, and, further, the newly immigrant adults may be affected. Generally, toxic residue should be shorter than the period pupa-adult emergence of the parasite which should not be touched by the treatment. Many examples could be mentioned (see: OBTEL 1961, AL-AZAWI 1966, STERN & V. D. BOSCH 1959, etc.).

Physiological selectivity originates from an inherent physiological difference in the susceptibility of hosts and natural enemies to a toxicant, i.e. when a pesticide is preferentially more poisonous to pest species than to natural enemies (BARTLETT 1964).

We have already mentioned that a fully selective insecticide with respect to aphid parasites cannot occur as the parasite developmental stages occurring inside living aphids are, in every case, affected simultaneously with the host. Physiological selectivity can occur with respect to aphids and parasite adults.

- Main attributes of a selective insecticide - A selective insecticide would, in general,

by preserving natural enemies, have the effect of throwing the balance back in favour of the natural enemies (SMITH & HAGEN 1959). A selective insecticide should not eliminate the population of the pest, but it should reduce it below the economic threshold, the natural enemies not being touched by the treatment in both cases. As mentioned by SMITH & HAGEN, selective treatment should be applied whenever the aphids population reached the economic threshold regardless of the existing status.

— Problems of application — We can summarize the problems arising with the application of insecticides in relation to aphid parasites as follows:

A certain part of the population of aphids (subeconomic levels) must survive the treatment and reproduce normally to allow the parasite population to find the host and to occur in the ecosystem.

Aphid biology, seasonal history namely must be evaluated in relation to the given ecosystem. In annual crops the aphids immigrate to the fields and they are only gradually followed by the parasites. It is possible to treat the plot in the period of aphid immigration to reduce the aphid number and prevent a possible outbreak irrespective of the parasites, as they are absent in the field at the moment.

Even a good selective action of an insecticide cannot be completely selective as a part of the parasite progeny occurs in living aphids which are influenced by the treatment regardless of whether they are parasitized or not. Thus, selectivity of insecticides should be related to mummified aphids and to parasite adults.

The insecticides must have a short residual action to prevent the killing of newly emerged and newly immigrant parasites.

The treatment must be well timed to coincide with the prevalent occurrence of the required parasite stage. Residual action must be taken into consideration.

In large fields, where the possible influence of the neighbourhood is low, modification of treatment practices should be used to allow the parasite occurrence inside these plots. Strip and spot treatment are believed to be most useful.

If the aphid vectors are to be controlled, their population should practically be eliminated during the possibly critical period. As most of the aphids are dangerous as early immigrants, the parasites do not usually occur simultaneously with them in the annual crop fields. In control of vectors, parasites have an additional role in limiting the host numbers in untreated ecosystems.

Parasites are not the only members of the aphid-natural enemy food chain. The selective action of the insecticides both to the parasites and other members of the chain such as predators should be considered.

— Treatment practices may considerably influence the effect of an insecticide on parasite populations in a given area.

— Complex treatment — Complex treatment of a field covers the whole field irrespective of whether some plots are more or less infested by the pest aphid. Complex treatment practice does not allow the present parasite population to survive in the case that a non-selective insecticide was used. This causes the well known state of a quick new outbreak as aphids immigrate and reproduce very rapidly and much earlier than the parasites in the treated area.

If a complex treatment was made with a selective insecticide, the parasite mummies or adults surviving, the population of parasites also partially decreases as a part of the killed aphids includes also the parasite larvae. However, the presence of mummies and/or adults allows a relatively quick increase of the parasite population.

— Partial treatment — Partial treatment allows a much closer manipulation of host-parasite population relations in the area than a complex treatment.

1. Spot treatment. As a rule, at least in the initial stages of an outbreak, the aphids outnumbering occur in spotty patterns, which are known, e.g., in alfalfa fields

infested by *Acyrtosiphon pisum* or *Therioaphis trifolii*, while in a great part of the field the pest population may be on subeconomic levels. The treatment in the outbreak plots reduces the aphid numbers to subeconomic levels, the action of parasites being favoured.

2. Strip treatment has basically the same role as the spot treatment, but is technically less difficult, as aphid outbreak plots are not selected. It seems to be preferable in extensive fields.

If there are plant groups of a heterogeneous character such as ornamentals, which may be useful in parasite conservation due to the occurrence of alternative hosts, such plots naturally are not treated.

- The neighbourhood of the treated plot - Treatment practices should be classified with respect to the neighbourhood of the treated plot. If the neighbourhood includes chronic or at least temporary parasite foci, we can expect that the parasites will soon partially reduce the pests in these plots, while overpopulation could be expected in the central parts of the field and chemicals should be applied there.

The neighbourhood seems to be important in smaller fields while in extensive plantations modification of the treatment is necessary.

- Effect on parasites. Chemical treatment should be also dealt with, with respect to the origin of parasites of the given pest aphid.

Indigenous parasites are usually well synchronized with the occurrence of their aphid hosts as well as with the action of other natural enemies of the given pest, although this coincidence may considerably be obscured by cultural environments. Consequently, proper application of an insecticide is easier to re-establish the favourable host-parasite population relations. Two examples may be mentioned. During the heavy outbreaks of *Acyrtosiphon pisum* on alfalfa in Czechoslovakia, UBRTEL (1961) recognized that in a certain period of the season the indigenous parasite, *Aphidius ervi*, is rather effective and can influence the pest population. Consequently, application of insecticides was proposed to be well timed, at the period when most of the parasites were inside the mummified aphids, protected by the aphid skin. Further, insecticides with very short residual action were recommended to prevent the killing of newly emerging parasites. Another example, from Iraq, is reported by AL-AZAWI (1966). The indigenous parasite of *Hyalopterus pruni* on apricot was highly effective in some periods of the season, correct application of selective insecticide should favour its pressure on pest population for the rest of the season. Indigenous parasites have a great advantage in that if they are eliminated in a certain area through the application of a non-selective insecticide, they occur in other ecosystems from which they can gradually re-invade the given treated plot. Consequent changes in chemical control can improve the situation.

In the case of an introduced parasite species, care must be taken with respect to chemical control mainly because these species are not so well established in various ecosystems of the area as the indigenous species. Chemical treatment should be avoided at the colonization sites, and also in established parasite populations the selective insecticide application should be carried out very carefully to prevent the elimination of the newly established populations. This risk is considerably lower in perennial crops such as alfalfa, as the parasites occur here perennially even if they did not establish themselves in the neighbourhood of the fields. Naturally, a chemical control program must be modified with respect to the integration of control measures. The development of integrated control of *Therioaphis trifolii* in California is a very typical example, where the originally single chemical control of the newly introduced pest was gradually replaced by integrated control, where the chemicals are applied only to re-establish the favourable host-parasite (natural enemy) ratio.

Interval between treatment and sampling and number of aphids and parasites per 300 square feet and aphid parasitism (%)

Material and ounces per acre	1 Day			5 Days		
	No. Aphids	No. Adult P. palitans & T. utilis	Parasitism /300 IV. -Instar Nymphs (%)	No. Aphids	No. Adult P. palitans & T. utilis	Parasitism /300 IV. -Instar Nymphs (%)
Parathion, 4	21,123	0	56	41,450	18	18
Parathion, 6	22,973	0	48	42,498	1	16
Untreated	23,053	10	49	25,567	276	23

Table 17. Effect of parathion sprays on parasitized and non-parasitized *Therioaphis trifolii* and two parasites—*Praon exoletum* (= *palitans*) and *Trioxys complanatus* (= *utilis*). (STERN, 1962).

The introduced parasites, at least in the early period of their establishment, usually seem to be less synchronized with the host as well as with the action of other natural enemies. The proper application of chemicals is therefore also more difficult.

—*Effect of insecticides on separate developmental stages of parasites.* The aphidid parasites, being typical parasitoids, have a different relation to the host during the developmental stages of their life. These different relations are responsible for the different action of insecticides on their separate developmental stages.

The egg and lower instar larvae live inside the living hosts and seem to be affected equally like the host aphid. Non-parasitized and parasitized aphids containing parasite eggs or lower instar larvae will be reduced by an insecticidal treatment to an equal degree. A further development of aphid population after the treatment will be more rapid, as only a low number of parasite larvae that survived the treatment will pupate and produce parasite adults which lay eggs and cause an increase in parasite density. This situation was documented experimentally by STERN (1962) (Table 17). Naturally, immigration of parasites from the neighbourhood is responsible for a somewhat greater increase of parasite density than would occur in an isolated ecosystem.

The last instar larva, prepupa and pupa occur inside the mummy or mummy plus cocoon, or at least inside a cocoon. The mummy represents considerable protection of the parasite against the influence of insecticides, at least of some of them and of some of their concentrations (see: BARTLETT 1958, Table 18). This fact was observed by a number of authors (STERN & V. D. BOSCH 1959, LOWE 1964, KATO & SHIGA 1964, SHOREY 1963, OBTEL 1961, etc.).

The influence of the same insecticidal concentration on mummified aphids may differ in the laboratory and in the field as shown by OBTEL (1961), the lower influence in field conditions being probably due to the effect of meteorological factors.

The adult stage is the only developmental stage of the parasite which lives a truly free mode of life relatively independent of the host. Many authors agree that the adult stage is the most sensitive stage with respect to the insecticides. For example, according to STERN, V. D. BOSCH & BORN (1958), various concentrations of insecticides (parathion, malathion, phosdrin, trithion, systox) were toxic to the parasite adults although to a different degree, but none of the tested sprays affected the parasite cocoons (*Therioaphis trifolii*, *Praon exoletum*). Similarly, STERN & V. D. BOSCH (1959) showed that these parasites of *Th. trifolii* can survive non-selective treatments in the

Material	Pounds actual toxicant / gal. water	% mortality of parasites
Demeton	0.250	68
	.175	41
Parathion	0.125	100
	.063	84
	.031	70
Malathion	1.000	100
	.500	82
	.250	88
	.125	59
Check		20

Table 18. Relative toxicity of aphicide materials to pupae of *Praon exoletum* (= *palutans*) after direct spray application to mummified host bodies (*Therioaphis trifolii*) in the laboratory (BARTLETT, 1958).

more resistant pupal stage. SHOREY (1963) observed the same situation in *Diaeretiella rapae*, and OBRTEL (1961) in *Aphidius ervi*, a native parasite of *Acyrthosiphon pisum* in Czechoslovakia.

The different sensitivity of developmental stages of parasites to the influence of insecticides is of basic importance in an integrated control program. If the parasite populations are to be spared in the given area, the insecticides must be well selected and timed in application in dependence on the occurrence of the least sensitive parasite stage and they must have a short residual action to prevent the killing of emerged and immigrating parasite adults.

— *Mode of insecticide action.* Insecticides influence parasite populations in two ways:
— Direct action — Insecticides applied as sprays, stomach poison or in a contact way affect the parasites immediately after treatment or through the residues.

Low instar larvae are influenced in the same manner as their hosts. Most of them occur inside the host aphids present in the treated plot, while a lower number may immigrate to the ecosystem via alate parasitized aphids and be killed by the residual action of applied insecticides.

Developmental stages inside mummified hosts or in separate cocoons are, to a certain degree, protected against the immediate action of insecticides.

Parasite adults are influenced through direct contact of insecticides, or they are killed by stomach poisons when feeding on contaminated honeydew or through self-cleaning (see: FOLSOM & BONDY 1930, influence of calcium arsenate on the adults of *Lysiphlebus testaceipes*). The same is true of the parasites immigrating into the treated ecosystem from the neighbourhood or emerging after the treatment.

The selective action of various insecticides on the parasite adults and the degree of toxicity of the residues are very important because they basically influence the dispersal and successful occurrence of the parasites in a treated plot. For example, in the research on relative toxicity of various insecticides on parasites of *Therioaphis trifolii* the following results were obtained in California (STERN, V. D. BOSCH & BORN 1958) (Table 19): Parathion applied at 3.0 ounces and malathion at 9.7 ounces were extremely toxic to the parasite adults. Five hours after application approximately 97% of the adults were eliminated in the plots treated by these two chemicals.

Insecticide	Ounces toxicant per acre	Time of sampling after treatment and number of adult parasites per 100 insect net sweeps		
		5 hours	1 day	3 days
Parathion	3.0	11	108	410
Malathion	9.7	10	147	364
Phosdrin	1.0	39	206	397
Trithion	5.0	39	255	586
Systox	1.0	76	265	472
Systox	2.0	126	318	473
Untreated	..	384	331	629

Table 19. Relative toxicity of various insecticide sprays to the aphid parasite *Practolatus (= palitans)* (STERN, V.D. BOSCH & BORN 1958).

Phosdrin and trithion were slightly less toxic, killing about 90% of the adult parasites five hours after treatment. Systox applied at one ounce per acre gave 80% and two ounces 66% reduction in the parasite population, being conspicuously less drastic than the other materials tested. One day after application the adult parasites were still at relatively low levels in the plot treated with parathion and malathion, the two mentioned materials having residual toxicity and apparently killing many parasite wasps as they emerged from the cocoons or as they migrated into treated areas. Three days after application there was little difference in numbers of adult parasites in the various treated areas.

— Indirect action — The host population influenced by treatment influences the parasite population indirectly in the following ways:

1. Elimination of host population in a given plot through insecticide application means the secondary elimination of the parasite population too as the parasites, if they survived the treatment inside mummified aphids, etc., either disperse in searching for hosts in the neighbourhood or die without having the possibility to deposit their eggs.

2. Too severe a decrease of host population through insecticidal application can influence the intraspecific relations (competition) with superparasitism, dispersal, etc. of the parasites resulting.

3. The different sensitivity to the insecticide of different members of the aphid-natural enemy food chain may change the population relations of separate natural enemies, including the parasites. If predators are suppressed, parasites have a better possibility to increase and vice versa (see below).

Thus, insecticidal application should ideally reduce the host population to sub-economic levels, but not too much as to influence adversely the parasite (natural enemy) populations.

— Effect on interspecific relations. As we have mentioned in the introductory parts of this chapter the non- or poorly selective insecticide application may be followed by considerable changes in population densities of various pests and secondary outbreaks of non-target pests may follow. Such a situation was, for example, found by PIMENTEL (1961) in experimental Brassica oleracea communities, in which various insecticides were applied and the results compared with the situation in the control plots (Figs. 326-327, Table 20). As is obvious the application of insecticides to control Lepidoptera and flea beetles resulted in a rapid decrease of population densities of these target species, but the aphids increased rather significantly in numbers. A similar case was observed by BARTLETT & ORTEGA (1952): dosages of insecticides

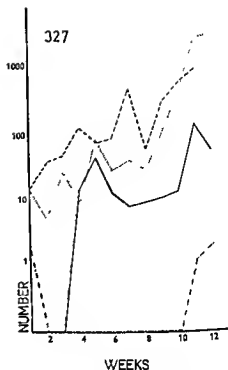
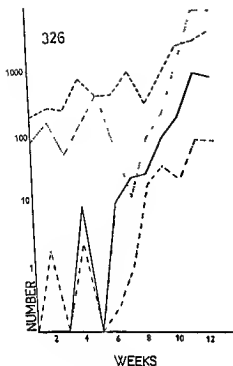


Fig. 326. The log number of aphids per 20,000 square inches of plant area in the control (—), DDT (---), rotenone (.....), and parathion (-.-.-) communities (PIMENTEL, 1961).

Fig. 327. The log number of parasites per 20,000 square inches of plant area in the control (—), DDT (---), rotenone (.....), and parathion (-.-.-) communities (PIMENTEL, 1961).

Taxon	Control	DDT	Rotenone	Parathion
Aphids	162.7	1,106.3	1,481.2	20.3
Lepidoptera	12.0	4.4	0.9	1.0
Flea beetles	1,107.1	3.5	5.3	1.5
Herbivores	643.5	3.4	2.0	1.0
Parasites	27.8	481.7	621.5	0.4
Predators	8.9	7.6	3.2	0.7

Table 20. The average taxa density per week recorded in the four experimental communities (PIMENTEL, 1961).

recommended for the control of codling moth on walnut in southern California have, in some instances, resulted in increased populations of *Chromaphys juglandicola*.

Nevertheless, in well advanced programs, where the pest populations are controlled through the use of selective insecticides, considerable changes must be made in the control program if a new pest appears in the community through incidental introduction. For example, as shown by STERN, V. D. BOSCH & BOWEN (1962), chemical control using parathion against *Hypera brunneipennis* (Boh.), a weevil pest on alfalfa, was commonly used in California. *Acyrthosiphon pisum*, which is a pest aphid on

alfalfa, was controlled in a similar way. However, in 1954 a new pest aphid, *Therioaphis trifolii*, appeared in California and soon became widely distributed in many districts. Serious problems appeared in consequence, because the aphid became resistant to parathion and, furthermore, parathion was detrimental to beneficial insects including the newly introduced parasites (*Praon exoletum*, *Trioxys complanatus*) of *Th. trifolii*. Consequently, where parathion treatment was used, there was a rapid flareback of the aphid and outbreaks of other pests. Therefore, parathion was replaced by demeton, but this insecticide had little effect on *Hypera* pest. Then, heptachlor was found to have no effect on beneficial insects and it was applied when *Acyrtosiphon pisum* was not a problem; however, it was later ascertained that it persisted on alfalfa longer. Further studies were undertaken during which parathion, Guthion, dimethoate, and methoxychlor were dealt with; it was recognized that only methoxychlor was useful as the aphid parasites survived higher dosage, while the insecticide was toxic to weevil larvae.

Even if we deal with the influence of a given insecticide on a given single pest - natural enemy food chain, significant differences as to its action on separate members of the food chain can be seen. Consequently, new relations among the populations of natural enemy species may temporarily develop. For example, the results of experiments undertaken by PIMENTEL (1961) may be mentioned. In these studies, the influence of various insecticides (DDT, rotenone, and parathion) (Figs. 326-327) on Brassica oleracea community, especially aphids and associated parasites and predators, was dealt with. Parasite densities were the highest in the DDT and rotenone communities and lowest in the parathion communities. The high parasite density in the rotenone and DDT communities was caused by the high cabbage aphid density in the control community, followed in abundance by the DDT, rotenone, and parathion community. All insecticides were effective in suppressing the predator population and such reduction allowed the aphids to increase, subsequently, the dense aphid populations provided ideal conditions for parasites, which reached high density levels. This case clearly shows that insecticidal application may, in certain cases, be followed even by a great increase of parasite densities through the insecticide reduction of the predators.

- *Difficulties in interpretation.* It is a common mistake, in the evaluation of an experimental program, to think that the decrease of a parasite population is considered to be due exclusively to the influence of insecticidal treatment. Incidentally, the problem is more complicated. Seasonal changes in parasite population density, action of hyperparasites, interspecific relations, changes in sex ratio (see: natural limitation), all these factors are responsible for changes in the parasite population density independent of the action of insecticide and they may obscure the true influence of the treatment. Furthermore, as shown by SHOREY (1963), there may be a direct insecticide induced mortality, or feeding on insecticide affected host, or starvation or migration after the host species has been eliminated.

- *Review of insecticides*

- Barthrin - SHANDS et al., 1965, Maine, potato, potato aphids, parasites.

- Bayer 29493 - SHOREY, 1961, California, peppers, *Myzus persicae*, *Aphidius matricariae*.

- Bayer 30911 - SHOREY, 1961, California, peppers, *Myzus persicae*, *Aphidius matricariae*. SHOREY, 1963, California, peppers, *M. persicae*, *A. matricariae*.

- BHC - BARTLETT, 1958, California, alfalfa-laboratory, *Therioaphis trifolii*, *Praon exoletum*, *Trioxys complanatus*. BARTLETT, 1964, California, aphid parasites. SEN, 1953-4, India, *Aphis fabae*, parasites. WAY, 1949, Gr. Britain, laboratory, *Brevicoryne brassicae*, *Myzus persicae*, *Diuraphis rapae*, *Aphidius matricariae*.

- Bildrin-R - SHANDS et al., 1965, Maine, potato, potato aphids, parasites.
- Bordeaux mixture - BARTLETT, 1964, California, aphid parasites.
- Calcium arsenate - BARTLETT, 1964, California, aphid parasites. FOLSOM & BONDY, 1930, U.S.A., *Aphis gossypii*, *Lysiphlebus testaceipes*.
- Carbaryl - SHANDS et al., 1965, Maine, potato, potato aphids, parasites.
- Carbophenothion - SHANDS et al., 1965, Maine, potato, potato aphids, parasites.
- Chlordane - BARTLETT, 1964, California, aphid parasites.
- Chlorfion-R - SHANDS et al., 1965, Maine, potato, potato aphids, parasites.
- Cryolite - BARTLETT, 1964, California, aphid parasites.
- DDT - BARTLETT, 1964, California, aphid parasites. V. D. BOSCH, SCHLINGER & HAGEN, 1962, California, walnut, *Chromaphis juglandicola*, *Trioxys pallidus*. MUMFELL, 1961, N.Y., Brassica oleracea, *Myzus persicae*, *Lipaphis pseudobrassicae*, *Brevicoryne brassicae*, *Diurictiella rapae*. POTTER & HERKINS, 1946, Gr. Britain, Brassica sp., *Brevicoryne brassicae*, *Diurictiella rapae*. PRINCIPAL et al., 1967, Italy, apple, *Dysaphis plantaginea*, *Trioxys angelicae*, *Aphidius fuscipes*. SIN, 1953-4, India, *Aphis fabae*, parasites. SHANDS et al., 1965, Maine, potato, potato aphids, parasites. SHOREY, 1963, California, Brassica sp., *Brevicoryne brassicae*, *Diurictiella rapae*. WAY, 1949, Gr. Britain, Brassica sp., *Brevicoryne brassicae*, *Diurictiella rapae*. WILSON, 1948, Ohio, maize, *Rhopalosiphum maidis*, *Lysiphlebus testaceipes*.
- DDVP - SHANDS et al., 1965, Maine, potato, potato aphids, parasites.
- Demeton - BARTLETT, 1958, California, citrus, citrus aphids, *Lysiphlebus testaceipes*. BARTLETT, 1958, California, alfalfa, *Therioaphis trifolii*, *Praon exoletum*, *Trioxys complanatus*. OBRETEL, 1961, Czechoslovakia, alfalfa, *Acyrtosiphon pisum*, *Aphidius erii*. SHANDS et al., 1965, Maine, potato, potato aphids, parasites. SHOREY, 1963, California, Brassica sp., *Brevicoryne brassicae*, *Diurictiella rapae*.
- Demeton methyl - BONNELMAISON, 1962, France, Brassica sp.-laboratory, *Brevicoryne brassicae*, *Diurictiella rapae*.
- Diazinon - SHANDS et al., 1965, Maine, potato, potato aphids, parasites. SHOREY, 1961, California, peppers, *Myzus persicae*, *Aphidius matricariae*. SHOREY, 1963, California, Brassica sp., *Brevicoryne brassicae*, *Diurictiella rapae*. SHOREY & HALE, 1963, California, peppers, *Myzus persicae*, *Aphidius matricariae*.
- Dibrom - SHOREY, 1961, California, peppers, *Myzus persicae*, *Aphidius matricariae*.
- Dilan - SHOREY, REYNOLDS & ANDERSON, 1962, California, Brassica sp., *Brevicoryne brassicae*, *Myzus persicae*, *Diurictiella rapae*.
- Dilan-R - BARTLETT, 1964, California, aphid parasites.
- Dimefox - SHANDS et al., 1965, Maine, potato, potato aphids, parasites.
- Dimethoate - BONNELMAISON, 1962, France, Brassica sp., *Brevicoryne brassicae*, *Diurictiella rapae*. SHOREY, 1961, California, peppers, *Myzus persicae*, *Aphidius matricariae*. SHOREY, 1963, California, Brassica sp., *Brevicoryne brassicae*, *Diurictiella rapae*. SHOREY, 1963, California, peppers, *Myzus persicae*, *Aphidius matricariae*. SHOREY & HALE, 1963, California, peppers, *Myzus persicae*, *Aphidius matricariae*. STERN, V. D. BOSCH & BOWEN, 1962, California, alfalfa, *Acyrtosiphon pisum*, *Therioaphis trifolii*, *Aphidius smithi*, *Praon exoletum*, *Trioxys complanatus*, *Lysiphlebus testaceipes*.
- Di-synton - SHOREY, 1963, California, peppers, *Myzus persicae*, *Aphidius matricariae*. SHOREY & HALE, 1963, California, peppers, *Myzus persicae*, *Aphidius matricariae*.
- Di-synton-R - SHANDS et al., 1965, Maine, potato, potato aphids, parasites.
- Dylox - SHOREY, 1961, California, peppers, *Myzus persicae*, *Aphidius matricariae*.
- Endosulfan - SHANDS et al., 1965, Maine, potato, potato aphids, parasites. SHOREY, 1963, California, Brassica sp., *Brevicoryne brassicae*, *Diurictiella rapae*. SHOREY & HALE, 1963, California, peppers, *Myzus persicae*, *Aphidius matricariae*.
- Endothion - BONNELMAISON, 1962, France, Brassica sp., *Brevicoryne brassicae*,

- Diaeretiella rapae*. SHANDS et al., 1965, Maine, potato, potato aphids, parasites.
- Endrin - PIMENTEL, 1961, N.Y., Brassica oleracea, *Myzus persicae*, *Lipaphis pseudobrassicae*, *Brevicoryne brassicae*, *Diaeretiella rapae*. SHANDS et al., 1965, Maine, potato aphids, parasites.
 - Ethion - SHANDS et al., 1965, Maine, potato, potato aphids, parasites. SHOREY, 1961, California, peppers, *Myzus persicae*, *Aphidius matricariae*. SHOREY, 1963, California, Brassica sp., *Brevicoryne brassicae*, *Diaeretiella rapae*.
 - Fosfotion - HODEK et al., 1966, Czechoslovakia, *Aphis fabae*, laboratory, *Praon abjectum*, *Lysiphlebus fabarum*. ZELNY, 1964, Czechoslovakia, *Aphis fabae*, laboratory, *Praon abjectum*, *Lysiphlebus fabarum*.
 - GC-4072 - SHOREY, 1961, California, peppers, *Myzus persicae*, *Aphidius matricariae*.
 - Guthion - SHOREY, 1961, California, peppers, *Myzus persicae*, *Aphidius matricariae*. SHOREY, 1963, California, peppers, *Myzus persicae*, *Aphidius matricariae*. STERN, V. D. BOSCH & BOWEN, 1962, California, alfalfa, *Acyrtosiphon pisum*, *Therioaphis trifolii*, *Aphidius smithi*, *Praon exoletum*, *Trioxys complanatus*, *Lysiphlebus testaceipes*.
 - Guthion-R - SHANDS et al., 1965, Maine, potato, potato aphids, parasites.
 - HETP - SEN, 1953-4, India, *Aphis fabae*, parasites.
 - Intration - HODEK et al., 1966, Czechoslovakia, *Aphis fabae*, laboratory, *Praon abjectum*, *Lysiphlebus fabarum*. ZELNY, 1964, Czechoslovakia, *Aphis fabae*, laboratory, *Praon abjectum*, *Lysiphlebus fabarum*.
 - Isolan - BONNEMAISON, 1962, France, Brassica sp., *Brevicoryne brassicae*, *Diaeretiella rapae*. PRINCIPI et al., 1967, Italy, apple, *Aphis pomi*, *Trioxys angelicae*.
 - Lead arsenate - BARTLETT, 1964, California, aphid parasites. WILSON, 1960, Australia, Brassica sp., *Brevicoryne brassicae*, *Diaeretiella rapae*.
 - Lindane - BARTLETT, 1958, California, alfalfa, *Therioaphis trifolii*, *Praon exoletum*, *Trioxys complanatus*.
 - Malathion - BARTLETT, 1958, California, alfalfa, *Therioaphis trifolii*, *Praon exoletum*, *Trioxys complanatus*. OBRIEL, 1961, Czechoslovakia, alfalfa, *Acyrtosiphon pisum*, *Aphidius ervi*. PIMENTEL, 1961, N.Y., Brassica oleracea, *Myzus persicae*, *Lipaphis pseudobrassicae*, *Brevicoryne brassicae*, *Diaeretiella rapae*. STERN & V. D. BOSCH, 1959, California, alfalfa, *Therioaphis trifolii*, *Praon exoletum*, *Trioxys complanatus*. STERN, V. D. BOSCH & BORN, 1958, California, alfalfa, *Therioaphis trifolii*, *Praon exoletum*.
 - Menazon - SHANDS et al., 1965, Maine, potato, potato aphid, parasites. SHOREY, 1963, California, peppers, *Myzus persicae*, *Aphidius matricariae*.
 - Metasystox - LOWE, 1958, N. Zealand, Brassica sp., *Brevicoryne brassicae*, *Diaeretiella rapae*.
 - Meta-systox-R - SHANDS et al., 1965, Maine, potato, potato aphids, parasites. SHOREY, 1963, California, peppers, *Myzus persicae*, *Aphidius matricariae*.
 - Metation - HODEK et al., 1966, Czechoslovakia, *Aphis fabae*, laboratory, *Praon abjectum*.
 - Methoxychlor - BARTLETT, 1964, California, aphid parasites. STERN, V. D. BOSCH & BOWEN, 1962, California, alfalfa, *Acyrtosiphon pisum*, *Therioaphis trifolii*, *Aphidius smithi*, *Praon exoletum*, *Trioxys complanatus*, *Lysiphlebus testaceipes*.
 - Methylparathion - PRINCIPI et al., 1967, Italy, apple, *Aphis pomi*, *Dysaphis plantaginea*, *Trioxys angelicae*, *Aphidius fici*.
 - Mevinphos - BONNEMAISON, 1962, France, Brassica sp., *Brevicoryne brassicae*, *Diaeretiella rapae*.
 - Nicotine - MORRILL, 1921, U.S.A., *Aphis gossypii*, *Lysiphlebus testaceipes*. PRINCIPI et al., 1967, Italy, apple, *Aphis pomi*, *Trioxys angelicae*. RICHARDSON & CASANGES, 1942, U.S.A., *Myzus persicae*, *Aphidius matricariae*.

- Trithion - SHOREY, 1961, California, peppers, *Myzus persicae*, *Aphidius matricariae*. STERN & V. D. BOSCH, 1959, California, alfalfa, *Therioaphis trifolii*, *Praon exoletum*, *Trioxys complanatus*. STERN, V. D. BOSCH & BORN, 1958, California, alfalfa, *Therioaphis trifolii*, *Praon exoletum*.

- Union Carbide 10854 - SHOREY, 1963, California, peppers, *Myzus persicae*, *Aphidius matricariae*.

- Vamidothion - BONNEMAISON, 1962, France, Brassica sp., *Brevicoryne brassicae*, *Diaeretiella rapae*.

- Zectran - SHOREY, 1963, California, Brassica sp., *Brevicoryne brassicae*, *Diaeretiella rapae*. SHOREY, REYNOLDS & ANDERSON, 1962, Brassica sp., *Brevicoryne brassicae*, *Myzus persicae*, *Diaeretiella rapae*.

- Zectran-R - SHANDS et al., 1965, Maine, potato, potato aphids, parasites.

- Various insecticides - ADARVE, 1965 (paper unknown to the author). KATO & SHIGA, 1964, Japan, cereals, *Sitobium avenae*, parasites. LOWE, 1964, N. Zealand, Brassica sp., *Brevicoryne brassicae*, *Diaeretiella rapae*. PROVERBS, 1954, Canada, cherry, *Myzus cerasi*, *Lysiphlebus testaceipes*, *Ephedrus persicae*.

- PHYSICAL CONTROL. Irrigation has a great influence on the microclimate and conditions of the plants. This change of environmental conditions influences the aphids generally in two ways:

1. Negatively: species preferring a drier microclimate disappear or occur to a smaller extent in the given area, they are generally rare species or their population levels are low.

This can be easily recognized in the newly cultivated irrigated virgin lands, where a number of semi-desert and steppe species is closely attached to other virgin localities.

Nevertheless, this can be observed in cultivated lands too. According to STEINER (1966), important differences were seen when dry and humid apple orchards in Switzerland were compared with respect to pest aphid occurrence: *Dysaphis plantaginea*, one of the key pest aphids, became a pest as a rule only in dry territories.

The period of irrigation may also be important as to aphid pest occurrence. According to JONES (1944) early irrigation was found to be an effective method of controlling the root aphids on sugar beet in Colorado. These observations can be also well illustrated by the fact that in a certain area such as C. Europe the root aphids are more common in dry springs, while they are relatively rare under rainy spring conditions.

2. Positively: contrary to the above mentioned cases, a number of aphid species prefer the more humid microclimate developed by irrigation. This can be observed in the newly cultivated and irrigated virgin areas, where a number of species concentrate just on the cultivated plots, as the plant conditions occurring there are much more suitable than in dry natural environments. Consequently, there is a much higher population density in the irrigated crop areas.

Irrigation extends, in some instances at least, till the growing season in arid areas and this extends the length of time over which the pest can increase; this may permit a species to increase to economic levels (SMITH 1959).

The intensity of irrigation is also responsible for the conditions of the host plant and may make it more or less suitable as food for aphids (DAVIS et al. 1957).

The influences of irrigation on aphid populations are rather important for aphid control as the integrated control will exhibit various modifications depending on irrigation. We must keep in mind that irrigation is above all to enhance agricultural production through the change of environmental conditions, but, as the results of various authors have shown, it may be usefully modified as one of the means of integrated control.

Principal Pests of Alfalfa in California	Economic Threshold	Major Natural Enemies	Selective Control Measures
Spotted Alfalfa Aphid <i>Therioaphis maculata</i>	* In spring 40 aphids/Stem In summer 20 aphids/Stem	Trioxys Praon Aphelinus	2-3 weeks System/Acre DO NOT TREAT FIRST THREE CUTTINGS IN FOLLOWING RATIOS
		Coccinellids	STANDING ALFALFA Lady Beetles Aphids per per 5000 Stem * Adult to 5-10 Aphids 3 larvae to 40 Aphids OR STUBBLE 6 larvae to 50 Aphids
Pea Aphid <i>Acyrthosiphon pisum</i>	Alfalfa 10 inches 40-50 Aphids/Stem 15 inches 70-80 Aphids/Stem 20 inches 100 Aphids/Stem	Aphidius	Same as above for Spotted Alfalfa Aphid

* Nearly all alfalfa is now resistant varieties

Fig. 328. A summary on integrated pest control on alfalfa in California showing the principal pests, their economic threshold, natural enemies and selective control measures to be taken when natural enemies are inadequate (STERN, 1966).

Besides its influence on the occurrence of pest aphids as to the number of species and their population densities, irrigation also influences the number of natural enemies present and their population levels. Furthermore, the population relations among the separate natural enemies can change as well due to their different requirements on microenvironmental conditions: it is known, for example, that the introduced parasites of *Therioaphis trifolii* became distributed just because of the microclimate in various alfalfa growing districts in California.

~ RELATIONSHIP OF SEPARATE MEASURES. The peculiarities of the ecosystem, the pest aphid, natural enemies (parasites) and the agricultural activity of man are so varied in mutual relations that it is obvious how the relationship of separate control measures must be. In some cases, biological or cultural control prevails, in others the chemical control is the best measure of supporting the effect of natural enemies. For this reason, we mention here two characteristic examples. The first one is the integrated control of *Therioaphis trifolii* on alfalfa in California, as briefly summarized by STERN (1966). This program, developed on a well prepared theoretical basis, has been put into practice and widely applied in California. *Th. trifolii*, which is now of little importance on alfalfa hay, is shown along the major pests to emphasize the tremendous economic rewards that can be obtained from integrated pest control (Fig. 328). When this pest first arrived in California from the Middle East (1954), it spread rapidly and threatened the entire alfalfa industry. Through a cooperative effort, this species was reduced to a minor status within six years by scientific research and by educating the growers. This was accomplished by the introduction of two parasites, the use of selective insecticides to hold the line until the parasites spread, and, resistant alfalfa varieties were developed and widely planted. Thus, in a few years, as the interwoven phases of this emergency project advanced from a total reliance on chemicals into a selective chemical-biological control program . . . , the

aphid problem in California decreased from 15 million dollars to 200 thousand dollars annually. This is an example of integrated control of an introduced pest on alfalfa, which was introduced in recent years and became widespread in California and many other districts of the Nearctic America.

Contrary to the mentioned aphid, *Myzus persicae*, although originally an introduced pest as well, has become a common member of California agroecosystems and natural stands. This aphid is a pest of a number of economic crops. SHOREY (1961, 1962, 1963, SHOREY & HALE 1963) developed an integrated control program of this aphid on peppers, where the aphid numbers, if reaching subeconomic levels (economic threshold) are decreased through the use of selective insecticides, while the natural enemies (especially parasites—*Aphidius matricariae*) keep the pest under economic levels for most of the season. This is a case of successful integrated control of pest (introduced) on an annual crop, where chemical control is used to re-establish a favourable balance between the pest and parasite populations.

As is obvious from the review of aphids-integrated control objects many other cases could be mentioned and classified, nevertheless, the above mentioned cases seem to be typical, differing sufficiently from each other to illustrate the different relationship of separate control measures in an integrated control program.

ZONES. In our opinion the integrated pest aphid control program may be applied in all the climatic zones of the world just because of its basic features of complexity and especially the dynamic relations of its separate components. There is no doubt that the separate climatic zones exhibit peculiar features with corresponding influences on crop growing and on the biology of aphids and parasites. Consequently, the separate control measures may be dominant to a various degree in supporting the action of natural enemies.

Good basic information on the development of an integrated control program in separate climatic zones can be obtained from the review of the control in separate countries and on different crops. The true picture is naturally obscured to a certain degree by the quantity of papers and intensity of work carried out on the matter in various institutes and countries. For example, the first successes obtained in the development and application of integrated control of the key alfalfa pest aphids in California seemed to document that an integrated control program will be the most successful in perennial forage-like crop communities, while annual crops were believed to be less suitable. However, several years later, other Californian workers have shown that integrated control programs are useful on annual crops too (peppers). Similarly, the greatest portion of papers dealing with integrated control problems have been written in California and thus naturally would show that this control would be most useful in the subtropics. Nevertheless, as we have mentioned, the eventual disadvantages of separate climatic zones with respect to pest aphid control are believed to be compensated by the relative dominance of separate control measures.

COUNTRIES. In this review we have mentioned all the cases of integrated control of aphids in which the parasites were dealt with as control agents. In our opinion it would not be justified to start the review with the period of the sixties of this century when integrated control was developed on a wide scientific basis. We know a number of cases when the authors came to an integrated control approach in quite an original way, their opinions were not further developed or generalized, but the results of their studies, recommendations or thoughts are useful for integrated control as developed at the present time.

– AUSTRALIA AND NEW ZEALAND. The main object of integrated control attempts was *Brevicoryne brassicae*, a pest aphid on cabbage. The influence of various insecticides on the aphid and its parasite, *Diaeretiella rapae*, were studied. According to WILSON (1960), the parasite provided a high degree of limitation of the aphid when no insecticide or lead arsenate only was applied to cabbage crop in the Australian Capital Territory. Rfcs.: Lowe 1958, 1964, Wilson 1960.

– CANADA. PROVERBS (1964) studied the influence of various insecticides on *Lysiphlebus testaceipes* and *Ephedrus persicae*, parasites of *Myzus cerasi*, in cherry orchards. Rfcs.: Proverbs 1964.

– CZECHOSLOVAKIA. *Aphis fabae* on sugar beet was the object of an integrated control program. The influence of various insecticides was studied and recommendations on parasite conservation were elaborated (HODEK et al. 1966, STARÝ 1962, ZELENÝ 1964).

Acyrtosiphon pisum. The influence of insecticides on the indigenous parasite, *Aphidius ervi*, was dealt with and recommendations on the use of insecticide elaborated (OBRTL 1961). The work on integrated control of the pest is in progress (HOZÁK in press, STARÝ in litt., research on the influence of cultural practices on indigenous and introduced parasites, etc.).

Hyalopterus pruni. Indigenous parasites and their role in pest limitation were studied, attempts on the introduction of another parasite undertaken, and projects on integrated control elaborated. The work is in progress (STARÝ 1964, 1965). Rfcs.: Hodek et al. 1966, Obertl 1961, Starý 1962, 1964, 1965, 1966, Zelený 1964.

– EGYPT. *Rhopalosiphum maidis* was the object of integrated control attempts, where the cultural practices were mostly stressed (sowing date, removing of weed plants, etc.). The parasites were only generally mentioned. Rfcs.: Hassan 1957.

– FRANCE. The influence of treatment on the indigenous parasites of apple pest aphids was studied by REGNIER (1923). BONNEMAISON (1962) undertook the laboratory research on the effect of insecticides on *Diaeretiella rapae*, a parasite of *Brevicoryne brassicae* on cabbage. Rfcs.: Bonnemaison 1962, Regnier 1923.

– GERMANY. *Acyrtosiphon pisum*. – BONESS (1958) studied the field effect of insecticides on the aphid and its indigenous parasite, *Aphidius ervi*.

Brevicoryne brassicae. – On the basis of detailed research of biology of the aphid and its indigenous parasite, recommendations on parasite conservation were elaborated (PAETZOLD & VATER 1966, SEDLAG 1959, 1964). Rfcs.: Boness 1958, Paetzold et Vater 1966, Sedlag 1959, 1964.

– GREAT BRITAIN. WAY (1949) studied the laboratory effects of various insecticides on *Brevicoryne brassicae* and *Myzus persicae* and their aphid parasites.

HUSSEY (1965) dealt with the possibilities of integrated control of greenhouse pests, including *Myzus persicae* and its parasite. Rfcs.: Hussey 1965, Way 1949.

– INDIA. SEN (1953-4) undertook field and laboratory experiments on the effect of various insecticides on *Aphis fabae* and its indigenous parasites. Rfcs.: Sen 1953-4.

– IRAQ. AL-AZAWI (1966) dealt with the natural limitation of *Hyalopterus pruni* by *Aphidius transcaspicus* in apricot orchards and proposed the timing of insecticide treatment to support the favourable host-parasite ratio. Rfcs.: Al-Azawi 1966.

– ITALY. The specific composition and main biological features of the parasites of citrus and peach aphids were studied by STARÝ (1964, 1966) and parasite conservation recommendations elaborated.

PRINCIPI et al. (1967) dealt with the effect of various insecticides on apple pests, *Dysaphis plantaginea* and *Aphis pomi*, and their parasites. Rfcs.: Principi et al. 1967, Starý 1964, 1966.

– JAPAN. KATO & SUGA (1964) studied the influence of insecticides on pest aphid on

cereals, *Sitobium avenae*, which was parasitized and mummified by the aphidiids. Rfcs.: Kato et Shiga 1964.

— NETHERLANDS. Considerable amount of work was done on the integrated control problems in orchards. The role of the parasites in natural limitation was mostly studied (EVENHUIS see rfcs.). The effect of cultural practices on the aphids and parasites was dealt with by POST (1962). Rfcs.: Evenhuis 1962, etc., Post 1962.

— PERU. Integrated control of cotton pest aphid, *Aphis gossypii*, is reported. Rfcs.: Adarve 1965, Boza Barducci 1965.

— POLAND. *Acyrtosiphon pisum* was the object of research of PIEKARCZYK & WEGOREK (1966). Natural limitation of this pest aphid on alfalfa was studied and recommendations of the timing of insecticide applications elaborated. Rfcs.: Piekarczyk et Wegorek 1966.

— SWITZERLAND. A great amount of work has been carried out on the integrated control problems in orchards. Nevertheless, only STEINER (1965) has dealt with the influence of insecticides on apple aphids and their indigenous parasite, *Ephedrus plagiator*. Rfcs.: Steiner 1965.

— U.S.A. Alfalfa aphids. Alfalfa aphids, *Acyrtosiphon pisum* and *Therioaphis trifolii*, were one of the example objects on which the integrated control was originally developed. In the program studies on control of the aphids by introduced parasites, as well as the influence of various insecticides on the host and parasites and influence of irrigation and cultural practices (cutting) were included. Complete integrated control has been developed and widely applied in praxis (references—see below).

Potato aphids. Influence of various insecticides on potato aphids and their indigenous and introduced parasites, and the influence of some cultural practices (weeding, timing of planting, strip cropping) were studied by SHANDS et al. (1965, SHANDS & LANDIS 1964) in Maine.

Brassica aphids. Influence of insecticides on *Brevicoryne brassicae* and *Myzus persicae* and their parasite, *Diaeretiella rapae*, was dealt with by SHOREY (1963, SHOREY, REYNOLDS & ANDERSON 1962). PIMENTEL (1961) studied the influence of insecticides on the Brassica single—and mixed—communities, special attention being paid to aphids and their parasites.

Aphids on peppers. SHOREY (1961, 1963, SHOREY & HALE 1963) developed and successfully applied in praxis an integrated control program on peppers, the chemical control being used for re-establishing the favourable balance between the pest aphid, *Myzus persicae* and its parasite populations.

Citrus aphids. The influence of insecticides on citrus pest aphids and their parasite, *Lysiphlebus testaceipes* was studied by BARTLETT (1958).

Walnut aphids. The influence of some pesticides, which were applied to control some other pests, on *Chromaphis juglandicola* and its introduced parasite, *Trioxys pallidus*, were reported by V. D. BOSCH, SCHLINGER & HAGEN (1962).

Research on the effects of various insecticides on various pest aphids and their indigenous parasites was undertaken by several authors: MORRILL (1921) *Aphis gossypii* and *Lysiphlebus testaceipes*; FOLSOM & BONDY (1930) *Aphis gossypii* and *Lysiphlebus testaceipes*, RICHARDSON & CASANGES (1942) *Myzus persicae* and *Aphidius matricariae*, WILSON (1948) *Rhopalosiphum maidis* and *Lysiphlebus testaceipes*.

In addition to the mentioned authors we should also mention the trend in cultural control developed originally by MARCOVITCH (1935), the strip farming program. Rfcs.: Bartlett 1958, v. d. Bosch 1959, 1965, 1966, v. d. Bosch, Lagace, Stern 1966, v. d. Bosch, Schlinger, Hagen 1962, v. d. Bosch et al., 1964, 1966, Davis et al. 1957, Folsom et Bondy 1930, Knowlton 1966, Marcovitch 1935, Morrill 1921, Pimentel 1961, Richardson et Casanges 1942, Schlinger et Dietrick 1960, Smith R. F. et Hagen

1959, 1960, 1965, 1966, Stern 1960, 1962, Stern, v. d. Bosch, Leigh 1964, Stern, v. d. Bosch 1959, Stern et al. 1960, Shands et Landis 1964, Shands et al. 1965, Shorey 1961, 1963, Shorey et Hale 1963, Shorey, Reynolds, Anderson 1962, Wiackowski 1960, Wilson 1948.

— U.S.S.R. Recommendations on the conservation of parasites in the orchards of the European part were elaborated by GUSYNINA (1958).

Integrated control of aphids on cotton is reported to be in progress in some districts of C. Asia. Rfcs.: Gusynina 1958.

HABITATS AND CROPS

— **Alfalfa.** Alfalfa, a perennial crop, represents a relatively stable agroecosystem, which includes a relatively low number of key pest species. These and other factors make the alfalfa crop one of the obviously most suitable objects for an integrated control program to develop.

Integrated control of pest aphids on alfalfa has been the subject of research of Californian workers for many years. Because the two aphid key pests, *Acyrtosiphon pisum* and *Therioaphis trifolii* represent introduced species, parasites from abroad were introduced and successfully established, their action being supported by the indigenous natural enemies, namely predators. The biological control is integrated with the use of selective insecticides, an irrigation program, and by the development of a special mowing system which allows the best conservation of natural enemies (parasites) and widely supports the existence of relative stability in the given ecosystem which would be strongly negatively influenced by the commonly used harvesting practices.

In Europe the main interest seems to be paid to the action of indigenous parasites whose effectiveness is supported by the use of selective insecticides, introduction of parasites from abroad and by the modification of cultural practices. Work on this problem is in progress (OBRETEL 1961, PIEKARCZYK & WEGOREK 1966, HOZÁK in press, STARÝ in litt.). Rfcs.: Bartlett 1958, v. d. Bosch 1965, 1966, v. d. Bosch, Lagace, Stern 1962, v. d. Bosch et al. 1959, 1964, 1966, Davis et al. 1957, Hozák in press, Knowlton 1966, Obretel 1961, Piekarczyk et Wegorek 1966, Schlinger et Dietrick 1960, Smith R. F. et Hagen 1965, 1966, Stern 1962, 1966, Stern et v. d. Bosch 1959, Stern, v. d. Bosch, Born 1958, Stern, v. d. Bosch, Bowen 1962, Stern, v. d. Bosch, Leigh 1964, Wiackowski 1960.

— **APPLE.** Research workers have paid great interest to the influence of modern cultural practices applied in apple growing on the main pests and their natural enemies (parasites) in Europe (POST 1962, WILDBOLZ 1965). Furthermore, within the frame of integrated control in apple orchards, the effect of various insecticides on the parasites has been dealt with (REGNIER 1923, PRINCIPI et al. 1967, STEINER 1965). Recommendations on parasite conservation in apple orchards were elaborated in the European part of the U.S.S.R. (GUSYNINA 1958). Rfcs.: Gusynina 1958, Post 1962, Principi et al. 1967, Regnier 1923, Steiner 1965, Wildbolz 1965.

— **BANANA.** A project on integrated control of aphids attacking bananas was elaborated by STARÝ (1966). On the basis of field observations the biological features of the pest aphid, *Pentaloma nigrovirens*, with respect to the damage caused to bananas were summarized. Multilateral control approach was recommended. Rfcs.: Starý 1966.

— **CABBAGE.** Most of the papers deal with the influence of various insecticides on the parasites of *Brevicoryne brassicae* and other key aphid pests attacking cabbage in various parts of the world.

In Germany, recommendations were elaborated to conserve the indigenous parasites through environmental modifications (SEDLAG 1959, 1964, PALTZOLD & VATER 1966). Rfcs.: Lowe 1958, 1964, Paltzold et Vater 1966, Pimentel 1961, Potter et Perkins 1946, Sedlag 1959, 1964, Shorey 1963, Shorey, Reynolds, Anderson 1962, Wilson 1960.

— CEREALS. The effect of various insecticides on mummified parasites of cereal pest aphid, *Sitobium avenae*, was studied in Japan (KATO & SHIGA 1964).

The influence of weeding on *Schizaphis graminum* and indigenous parasites was dealt with by PEAIRS & DAVIDSON (1956) in the U.S.A. Rfcs.: Kato et Shiga 1964, Peairs et Davidson 1956.

— CHERRY. The influence of various insecticides applied in the Canadian cherry orchards on the indigenous parasites of the pest aphid was the object of research of PROVERBS (1954). Rfcs.: Proverbs 1954.

— CITRUS. Projects on parasite conservation in the Italian Citrus orchards through environmental modification and use of alternative hosts were dealt with by STARÝ (1964, 1966).

Several recommendations on integrated control of citrus aphids of the world were elaborated by STARÝ (1967).

The influence of insecticides on the indigenous parasites of citrus pest aphids in California was the subject of research of BARTLETT (1958). Rfcs.: Bartlett 1958, Starý 1964, 1966, 1967.

— COTTON. Integrated control of cotton aphids was developed in Peru (ADARVE 1965, BOZA BARDUCCI 1965).

Attempts on the development of an integrated control program of key aphid pests of cotton are also reported from the Soviet C. Asia, where the aphids represent a serious economic problem. Rfcs.: Adarve 1965, Boza Barducci 1965.

— MAIZE. Integrated control, with prevalence of cultural practices (sowing data, weeding), as a means of pest aphid control on maize was proposed in Egypt (HASSAN 1957).

The influence of insecticides on *Rhopalosiphum maidis*, a pest aphid in Ohio, was studied by WILSON (1948). Rfcs.: Hassan 1957, Wilson 1948.

— PEACH, PLUM, APRICOT. As to pest aphids, the work concerning integrated control of pests seems to be concentrated on the problems of *Hyalopterus pruni*

STARÝ (1964, 1966) elaborated a project on parasite conservation in Italian orchards through the modification of the environment and use of alternative hosts.

H. pruni has been an object of biological control through attempts to introduce a parasite, *Aphidius trauascaspicus*, into Czechoslovakia. In this connection, several proposals on integrated control development were elaborated (STARÝ rfcs.).

In Iraq, where the effectiveness of the indigenous *Aphidius trauascaspicus* was found to be rather high in some periods of the season, the selective use of insecticides to support its action was proposed by AL-AZAWI (1966). Rfcs.: Al-Azawi 1966, Starý 1964, 1965, 1966.

— PEPPERS. Integrated control program of *Myzus persicae*, one of the key pests on peppers, was developed and successfully applied in praxis by SHOREY (1961, 1963, SHOREY & HALE 1963). Selective insecticides are used to suppress the increase in aphid population levels below the economic threshold and to re-establish the favourable aphid-indigenous parasite ratio. Rfcs.: v. d. Bosch 1965, Shorey 1961, 1963, Shorey et Hale 1963.

— POTATOES. Integrated control of aphids on potatoes was developed in Maine. Use of selective insecticides and modification of the environment (weeding, planting time, inter-cropping) was directed to support indigenous and to a lesser degree

introduced natural enemies (parasites). Rfcs.: Shands et Landis 1964, Shands et al 1965.

— SUGAR BEET. Integrated control of *Aphis fabae*, one of the key pests in Czechoslovakia, was mainly directed to the use of predators, while the parasite research was dealt with on a basic research level and only some recommendations on parasite conservation through modification of the environment were made. Rfcs.: Hodek et al., 1966, Starý 1962, 1966, Zelený 1964.

— WALNUT. *Chromaphis juglandicola*, an introduced pest on walnut in California, was an object of mainly biological control, but it was necessary to evaluate the effect of chemical control measures directed against other walnut pests. This work was undertaken by V. D. BOSCH et al. (1962) with respect to the conservation and effectiveness of *Trioxys pallidus*, an introduced parasite of the mentioned aphid. Rfcs.: V. D. Bosch, Schlinger, Hagen 1962.

If we summarize the integrated control of the key pest aphids on different crops it is obvious that integrated control programs were developed both in annual and perennial crops. Although there is a general opinion that perennial crops are more suitable for the development of integrated control programs because of a greater relative stability of the ecosystem, it seems that at least a more favourable state as to the host-parasite population relations can be reached through the use of integrated control programs in annual crops too.

APHIDS—CONTROL OBJECTS

— *Acyrtosiphon pisum*. BONESS, 1958, Germany, clover, *Aphidius ervi*, influence of Toxaphene. V. D. BOSCH, 1965, California, alfalfa, integrated control. V. D. BOSCH 1966, California, alfalfa, *A. smithi*, influence of cultural practices. V. D. BOSCH et al., 1966, California, alfalfa, *A. smithi*, influence of cultural practices. V. D. BOSCH, LAGACE & STERN, 1966, California, alfalfa, *A. smithi*, influence of cultural practices, strip cutting program. OBRTEL, 1961, Czechoslovakia, alfalfa, *A. ervi*, influence of Demeton and Malathion. PIEKARCZYK & WEGOREK, 1966, Poland, alfalfa, *A. ervi*, recommendations—the timing of treatment. SCHLINGER & DIETRICK, 1960, California, alfalfa, *A. smithi*, influence of cultural practices, strip cutting program. SMITH & HAGEN, 1965, California, alfalfa, *A. smithi*, influence of cultural and physical practices, cutting and irrigation. STERN, V. D. BOSCH & BOWEN, 1962, California, alfalfa, *A. smithi*, influence of parathion, Guthion, dimethoate, methoxychlor. STERN, V. D. BOSCH & LEIGH, 1964, California, alfalfa, *A. smithi*, influence of cultural practices, strip cutting.

— *Aphis fabae*. HODEK et al., 1966, Czechoslovakia, sugar beet and other host plants, parasite conservation projects, laboratory—influence of insecticides: *Praon abjectum*, fosfotion, intration, metathion, *Lysiphlebus fabarum*, fosfotion, intration. SEN, 1953-4, India, field and laboratory experiments, influence of HETP, parathion, BHC, DDT. ZELÉNY, 1964, Czechoslovakia, laboratory, *Praon abjectum*, *Lysiphlebus fabarum*, influence of fosfotion, intration and Soldep.

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— *Aphis pomi*. POST, 1962, Netherlands, apple, *Trioxys angelicae*, cultural practices. PRINCIPAL et al., 1967, Italy, apple, *Tr. angelicae*, influence of methylparathion, isolan, nicotine.

— *Brevicoryne brassicae*. BONNEMAISON, 1962, France, Brassica sp., *Diaperella rapae*, influence of demeton methyl I, endosulfon, mevinphos, vamidothion, dimethoate, isolan. LOWE, 1958, N. Zealand, Brassica sp., *D. rapae*, influence of metasystox.

- LOWE, 1964, N. Zealand, Brassica sp., *D. rapae*, influence of insecticides. PAETZOLD & VATER, 1966, Germany, Brassica sp., *D. rapae*, recommendations-parasite conservation. PIMENTEL, 1961, N.Y., Brassica oleracea, *D. rapae*, influence of DDT, rotenone, parathion, endrin, malathion. POTTER & PERKINS, 1946, Gr. Britain, Brassica sp., *D. rapae*, influence of DDT. SHOREY, 1963, California, Brassica sp., *D. rapae*, influence of demeton, endosulfan, dimethoate, phosphamidon, parathion, diazinon, phosdrin, DDT, zectran, ethion. SHOREY, REYNOLDS & ANDERSON, 1962, California, Brassica sp., *D. rapae*, influence of zectran, sevin, dilan. WAY, 1949, Gr. Britain, Brassica sp., laboratory, *D. rapae*, influence of DDT, BHC. WILSON, 1960, Australia, Brassica sp., *D. rapae*, influence of lead arsenate.
- *Chrouaphis juglandicola*. v. D. BOSCH, SCHLINGER & HAGEN, 1962, California, walnut, *Trioxys pallidus*, influence of DDT.
- *Dysaphis plantaginea*. PRINCIPI et al., 1967, Italy, apple, *Trioxys angelicae*, *Aphidius picipes*, influence of parathion, methylparathion, DDT.
- *Hyalopterus pruni*. AL-AZAWI, 1966, Iraq, apricot, *Aphidius transcaspicus*, recommendations-timing of treatment. STARÝ, 1964, 1965, 1966, Czechoslovakia, peach, plum, parasite conservation, recommendations-timing of treatment. STARÝ, 1964, Italy, peach, *Aphidius transcaspicus*, recommendations-parasite conservation.
- *Lipaphis pseudobrassicae*. PIMENTEL, 1961, N.Y., Brassica oleracea, *Diaeretiella rapae*, influence of DDT, rotenone, parathion, endrin, malathion.
- *Myzus cerasi*. PROVERBS, 1954, Canada, cherry, *Lysiphlebus testaceipes*, *Ephedrus persicae*, influence of insecticides.
- *Myzus persicae*. HUSSEY, 1965, Gr. Britain, *Aphidius matricariae*, possibilities-integrated control in greenhouses. PIMENTEL, 1961, N.Y., Brassica oleracea, *Diaeretiella rapae*, influence of DDT, rotenone, parathion, endrin, malathion. RICHARDSON & CASANGES, 1942, U.S.A., *Aphidius matricariae*, influence of nicotine. SHOREY, 1961, California, peppers, *Aphidius matricariae*, influence of thiodan, diazinon, parathion, dylox, sevin, rotenone, dibrom, guthion, dimethoate, trithion, ethion, phosphamidon, ronnel, Bayer 30911, GC-4072, Bayer 29493. SHOREY, 1963, California, peppers, *A. matricariae*, influence of dimethoate, di-synton, guthion, phorate, Bayer 30911, Menazon, Meta-systox-R, phosphamidon, Union Carbide 10854. SHOREY & HALE, 1963, California, peppers, *A. matricariae*, influence of dimethoate, di-synton, endosulfan, diazinon, parathion, phosphamidon. SHOREY, REYNOLDS & ANDERSON, 1962, California, Brassica sp., *Diaeretiella rapae*, influence of zectran, sevin, dilan. WAY, 1949, Gr. Britain, Brassica sp.-laboratory, *Aphidius matricariae*, influence of BHC.
- *Pentalonia nigroervosa*. STARÝ, 1966, integrated control projects.
- *Rhopalosiphum maidis*. HASSAN, 1957, Egypt, maize, cultural practices. WILSON, 1948, Ohio, maize, *Lysiphlebus testaceipes*, influence of DDT.
- *Schizaphis graminum*. PEAIRS & DAVIDSON, 1956, U.S.A., cereals, cultural practices.
- *Sitobium avenae*. KATO & SHIGA, 1964, Japan, cereals, hymenopterous parasites, influence of insecticides.
- *Therioaphis trifolii*. BARTLETT, 1958, California, alfalfa, *Praon exoletum*, *Trioxys complanatus*, influence of schradan, malathion, parathion, phosdrin, lindane, rotenone, toxaphene, BHC, TEPP, demeton, nicotine sulphate. v. D. BOSCH, 1965, California, integrated control. v. D. BOSCH et al., 1959, California, alfalfa, *Praon exoletum*, *Trioxys complanatus*, integrated control-insecticide application, cultural practices. v. D. BOSCH et al., 1964, California, alfalfa, hymenopterous parasites, influence of cultural practices-cutting. DAVIS et al., 1957, California, alfalfa, integrated control program. SCHLINGER & DIETRICK, 1960, California, alfalfa, influence of cultural practices on parasites-strip cutting. SMITH & HAGEN, 1965, California, alfalfa, influence

of irrigation and cutting on hymenopterous parasites. SMITH & HAGEN, 1966, California, alfalfa, integrated control. STERN, 1966, California, alfalfa, integrated control. STERN & V. D. BOSCH, 1959, California, alfalfa, *Praon exoletum*, *Trioxys complanatus*, influence of parathion, malathion, phosdrin, trithion, systox. STERN, V. D. BOSCH & LORN, 1958, California, alfalfa, *Praon exoletum*, influence of parathion, malathion, phosdrin, trithion, systox. STERN, V. D. BOSCH & BOWEN, 1962, California, alfalfa, hymenopterous parasites, influence of parathion, guthion, dimethoate, methoxychlor.

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- *Fruit tree aphids*. GUSYNINA, 1958, U.S.S.R.-Eur. part, recommendations-parasite conservation.

- *Potato aphids*. SHANDS et al., 1963, Maine, potato, parasite species, influence of insecticides, cultural practices-planting time, strip cropping. SHANDS & LANDIS, 1964, Maine, potato, parasite species, integrated control. SHANDS et al., 1965, Maine, potato, parasite species, integrated control, influence of DDT, endosulfan, barthrin, carbaryl, carbophenothion, chlorthion-R, DDVP, diazinon, endrin, endothion, ethion, guthion-R, parathion, toxaphene, zectran-R, demeton, meta-systox-R, menazon, di-synton-R, phorate, dimetox, bildrin-R.

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PARASITES-CONTROL AGENTS

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- *Aphidius matricariae*. HUSSEY, 1965, Gr. Britain, greenhouses, recommendations-integrated control. RICHARDSON & CASANCES, 1942, U.S.A., *Myzus persicae*, influence of nicotine. SHOREY, 1961, California, peppers, *M. persicae*, influence of thiodan, diazinon, parathion, dylox, sevin, rotenone, dibrom, guthion, dimethoate, trithion, ethion, phosphamidon, ronnel, Bayer 30911, GC-4072, Bayer 29493. SHOREY, 1963, California, peppers, *M. persicae*, influence of dimethoate, di-synton, guthion, phorate, Bayer 30911, menazon, meta-systox-R, phosphamidon, Union Carbide 10854. SHOREY & HALL, 1963, California, peppers, *M. persicae*, influence of dimethoate, di-synton, endosulfan, diazinon, parathion, phosphamidon. WAY, 1949, Gr. Britain, laboratory, *M. persicae*, influence of BHC.

- *Aphidius pisces*. PRINCIPi et al., 1967, Italy, apple, *Dysaphis plantaginea*, influence of parathion, methylparathion, DDT.

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- *Lysiphlebus fabarum*. HODEK et al., 1966, Czechoslovakia, *Aphis fabae*, parasite conservation projects, influence of fosfotion, intration-laboratory. ZELENÝ, 1964, Czechoslovakia, *A. fabae*, influence of fosfotion, intration, soldep-laboratory.
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- *Praon abjectum*. HODEK et al., 1966, Czechoslovakia, *Aphis fabae*, parasite conservation recommendations, influence of fosfotion, intration, metation-laboratory. ZELENÝ, 1964, Czechoslovakia, *A. fabae*, influence of fosfotion, intration, soldep-laboratory.
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California, alfalfa, *Th. trifolii*, influence of parathion, malathion, phosdrin, trithion, systox. WIACKOWSKI, 1960, integrated control.

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Multilateral Control of Aphids

In earlier times aphid control in a given crop or a given pest aphid was dealt with as a separate problem, while in recent years a complex approach has been generally required. Many authors have independently reported remarkable examples. An integrated control concept has been developed. However, the approach to some pests, namely aphids, needs a wider aspect, such as would cover the species in various ecosystems. For this reason, the multilateral approach, being defined as Multilateral aphid control concept, has been developed by the author to stress the importance of interrelations among the separate ecosystems with respect to pest aphid control.

MCLEOD (1937) observed that in greenhouses *Myzus persicae* will live on various parts of its host plants, but the parasite *Ephedrus persicae* attacks only the aphids on the more exposed parts of the plant. The aphids on more shady parts of the plant are not attacked. There is, however, another parasite, *Aphidius matricariae*, which prefers just these places.

These observations are important, to stress the significance of microenvironments in pest aphid control by parasites. We can confirm them by another example, that of *Myzus persicae* and its parasite *Diaeretiella rapae* as observed in a greenhouse in Czechoslovakia: the parasite attacks the aphid on larger and broad leaves, while in other parts or on other plants the aphid is attacked only slightly or not at all.

PEAIRS & DAVIDSON (1956) recognized that *Schizaphis graminum* causes severe damage to barley, oats and wheat. Its principal host plants are wheat and oats, but it can and does live on several kinds of grasses and other grain crops. Cultural control through destruction of wild grasses was recommended.

Therefore, they recognized that control of pests on cultivated crops does not solve the problem, the other ecosystems being important just as well in aphid control.

GRIFFITHS & THOMPSON (1957), dealing with aphid control in Florida citrus orchards, mentioned the necessity of repeating the treatments by chemicals in orchards to control the aphids. In this connection, aphids are mentioned to be seasonal pests attacking citrus only during a part of its growth period.

This means again that sources of citrus pest aphids occur perennially in the neighbourhood of orchards; the treatment represents a short-time protection and does not touch the pest beyond the borders of citrus orchard ecosystem.

V. D. BOSCH (1957): *Aphis craccivora*, *Acyrtosiphon pisum*, and *Therioaphis trifolii* are mentioned as pest aphids on alfalfa in California.

A similar situation can be found in C. and southern Europe, where there are significant differences in relations of separate aphid species to neighbouring ecosystems, seasonal history, prevalence, parasite complexes, etc.

V. D. BOSCH (1959): when searching for parasites of *Therioaphis trifolii* in the Old World, in the Middle East especially, he found that there are differences as to the

microhabitat in two species of parasites: *Praon exoletum* and *Trioxys complanatus*. These differences were also later proved experimentally by TORCE & MESSLINGER (1964).

The aphid has apparently a wider ecological range as to the microhabitats than its parasites in the Middle East. Were there only a single parasite species occurring or introduced in California, the aphid would be free of parasites in certain parts of its distribution area in dependence of its parasites occurrence possibilities.

SCHLINGER, HAGL & V. D. BOSCH (1960): *Chromaphis juglandicola* is expected to be controlled by an introduced parasite, *Trioxys pallidus*, in California. As the aphid attacks the walnut tree exclusively, it might be attacked by the parasite in all its distribution area.

Therefore, there being no full coincidence of host and parasite in their distribution in California, the aphid would exhibit some parts in its distribution area where the parasite would be absent.

LUZHETSKI (1960) and MAMONTOVA (1957): *Robinia pseudoacacia* and *Caragana arborens* were found to be seasonal sources of *Aphis craccivora*, a pest aphid on cotton in southern parts of the Ukraine and in C. Asia in the U.S.S.R. A high degree of parasitization on *Robinia* was observed (50-70 %), while it was low and gradual in cotton fields.

The significance of various ecosystems in which the aphid occurs during the season, with respect to aphid control on cotton, is well documented by this example. Control of aphid on cotton does not touch the sources of the pest in the neighbourhood.

WEISMANN et al. (1961): significance of the occurrence of *Aphis fabae* on its primary host plant, *Euonymus europaea* for the outbreaks of the aphid on sugar beet in Czechoslovakia is discussed and means of (chemical) control elaborated or recommended.

The aphid occurs in quite different ecosystems (forest edges and fields), their relationship with respect to aphid control is stressed. Our observations (STARÝ 1964) have shown that parasite complexes are different.

SMITH (1962): integrated control concept was elaborated. The significance of ecosystem is stressed; (see previous chapter).

SILANDS & LANDIS (1964) recognized the importance of wild host plants as sources of aphids that become pests on potatoes later in the season, recommendation for control in Maine being added.

Some light was thrown on the relations between various (field) ecosystems during the season, with respect to aphid control and parasite (natural enemy) occurrence.

DAIBER (1964) found that colonization and population of potatoes by *Myzus persicae* could not be avoided regardless of how early potatoes were planted in S. Africa (results somewhat different from those in other parts of the world). In the vicinity of an abundance of *M. persicae* host plants, in the vicinity of gardens namely, the colonization of potatoes started earlier, or more intensively at first than our in the veldt. *Macrosiphum euphorbiae* was found to occur in a similar way. It was recognized that both aphids find their host plants continuing to breed in the gardens throughout the year.

The significance of aphid sources and their occurrence in other ecosystems for aphid occurrence in potato fields is well documented by these observations.

When studying pest aphids on cotton in C. Asia, GULYEV (1965) found that sources of cotton pest aphids are in the neighbouring virgin semi-desert ecosystems. The significance of virgin semi-desert ecosystem for cotton growing is apparent.

STARÝ (1965) stressed the importance of *Hyalopterus pruni* host plants and habitat alternation with respect to integrated control. While chemical treatments are tech-

nically possible in orchard ecosystems, this is not the case of wild ecosystems, e.g. edges of deciduous woods, hedges or reeds on ponds.

KŘÍZ (1966): *Prunus domestica* as a primary aphid host plant and source of *Phorodon humuli* for dispersal of the pest to hop gardens in Czechoslovakia, is mentioned. The timing of treatment must be made in dependence on the emigration of aphids from plum trees. However, under certain conditions, the emigration is rather prolonged, with corresponding later difficulties in aphid control in hop gardens.

WAY (1966) touched the multilateral approach as well when dealing with dispersal of aphids with respect to their natural enemies. He mentioned that little is known about the natural limitation of aphid populations except over relatively short periods of time in a single field or on single plants. True limitation may depend on interactions over a very large area, especially for the species which attack ephemeral annual crops.

The significance of a "very large area", covering apparently several different ecosystems, is stressed. We can add that the same is true of the parasites, and, moreover, the parasites exhibit some other and often more complicated—being parasites—relations to their environment.

STARÝ (original observations): *Rhopalosiphum maidis* was found to be a pest of maize (sucking) and of sugar cane (vector) in Cuba, while occurring also on various wild grasses in the neighbourhood of plantations. Its economic significance is mainly in transmitting virus disease onto cane; it must, however, be controlled in other ecosystems from which it disperses to cane fields (maize, wild grasses).

Similarly, *Toxoptera aurantii* must be controlled in various ecosystems of tropical rain forest in Cuba, as it attacks a great number of other plants besides cocoa and coffee. The control of aphids in a plantation does not solve the question as their sources in the neighbourhood are untouched. A similar case is that of the same aphid in the Black Sea coastal area of the U.S.S.R., where it is a pest of Citrus and tea plantations. Other aphids in the tropics might be mentioned as further examples as well (*Pentalonia nigronervosa* on bananas, etc.).

STARÝ (1967): brief information on multilateral aphid control concept has been published.

Further numerous examples may be found in the chapter on foes of parasites.

APHID AND PARASITE BIOLOGY. 1. It is generally known that no sharp limits exist among different ecosystems in nature, various intermediary zones being distinguishable. There are different connections with respect to separate species. This opinion was also shown earlier by SMITH (1962). Similar laws are true also of the ecosystems of various crops—with agroecosystems. Aphids are a group of insects which are just rather typical in crossing the limits of various ecosystems, in connection with their facultative or obligatory host alternation for instance. Aphid parasites are a group which is more ecosystem-dependent due to the stronger dependence on the type of habitat.

2. Open and closed ecosystems. Many ecosystems are rather stable, the number of species present is relatively constant and it is difficult for a species to enter such a system, as the ecological relations between the organisms occurring here are rather fixed, a result of long evolution. On the other hand, the other ecosystems do not have similar fixed relations for various reasons, and a species may more easily join the community.

Aphids, being migratory organisms, are often seasonal inhabitants of certain ecosystems. It is necessary to stress the formerly mentioned fact that aphids were

originally members of closed ecosystems (forests) and this feature is still recognizable in the occurrence of some aphid groups of today. However, other aphid species are present in closed ecosystems such as forests during a certain part of the season, emigrating to other ecosystems—both closed and open ones. This feature gives aphids a peculiar position as to their control. The parasites, on the contrary, do not alternate habitats, being relatively habitat dependent: naturally, they have a certain dispersive potential which allows them to disperse from one related ecosystem to another.

3. Microenvironment is a further feature distinguishing aphid and parasite groups. Although being present in the same ecosystem, the parasites may be differentiated in dependence on aphid microenvironment, a certain part of a plant or a dried or more humid area of the ecosystem.

4. Host and parasite in various ecosystems. Principally, as is stressed in other chapters of this book, host (pest) and parasite may or may not coexist in an ecosystem during the whole season, the host aphid being responsible for the changes in the relations due to its migration, in other cases, coexistence may be relative or unequal (quiescent states either of host or parasite species).

MULTILATERAL LIMITATION. It is generally known that an insect species may have different average population densities, i.e. equilibrium positions, in different habitats. There are differences in food, shelter, natural enemies, or physical factors involved (DOUTT & DEBACH 1964). On the other hand, enemy action as a whole results from the complementary total sum of single species action differing in many ways (FRANZ 1964).

Aphids, the pest species namely, are just typical insects which occur commonly in different types of habitats. Better to say, in some climatic zones, the obligatory host alternation is also connected with the habitat alternation. Naturally, and thus is an illustration of the above mentioned general theses, they have different average population densities in these habitats as well. As we have already shown, there is mostly a strong difference between the parasite complexes in these habitats, i.e. in habitats of different kinds, besides, some habitats of the same or different kinds may be stable or unstable environments. The number of aphids on primary host plants influences the number of emigrating aphids and their initial occurrence on the secondary host plants. It is apparent that the seasonal history of an aphid species may be understood on the base of all the ecosystems in which it occurs during the season. Similarly, the complex action of natural enemies in nature means, in addition to others, that the given host aphid is theoretically attacked and limited by the natural enemies in all the ecosystems in which it occurs during the season.

With respect to the multilateral control concept, there is no doubt that a similar state, recommended to be reached by pest (aphid) control, occurs in a more or less perfect state in nature, with no interference of man. We have, therefore, in connection with the nomenclature used, distinguished (see natural limitation chapter) such a state existing without or with dependence on man as multilateral limitation and multilateral control respectively, defining the multilateral limitation as a result of complementary action of natural enemies in nature without the interference of man.

MULTILATERAL CONTROL CONCEPT Seasonal history and distribution of aphids and parasites may be said to put really the idea of multilateral control in our minds as the parasites (and other natural enemies) are able to find and attack aphids in the greatest part of habitats and microhabitats in which they occur, their limiting activity being therefore really multilateral, as we have already mentioned above. The control

of an aphid in a given plot or a crop, therefore, might be demonstrated as an apparent case of our ignorance of the conditions so nicely demonstrated to occur in nature.

The principles of the multilateral control concept may be briefly defined as follows: an aphid pest species must be controlled as a species (total population) in all the ecosystems in which it occurs during the season. Its occurrence in a given plot such as a cultivated crop field cannot be classified separately, but with respect to conditions in other ecosystems.

There is no doubt, however, that it is a real question whether we shall be able to "control" the species in all ecosystems. In some closed ecosystems namely, we perhaps shall be able to get only some information on the degree of limitation of an aphid species by parasites (natural enemies) rather than to put the species under control. Such information, however, could be of great significance for an integrated control program on cultivated crops.

ZONES. In our opinion, a multilateral control approach seems to be a necessary part of the integrated control program, being applicable in the same climatic zones. Nevertheless, there will be some differences connected with the seasonal history and occurrence of aphids and parasites in a given zone. General information in this respect may be obtained in the Bionomics and life-history chapter.

MULTILATERAL AND INTEGRATED CONTROL. It is generally agreed that integrated control must be developed around a certain crop and not around a single pest species (see: SMITH, 1962, STERN & FRANZ 1966, DE FLUITER 1967).

This statement is without any doubt quite correct. We must really deal with a crop field as with an ecosystem in which the species are in various relations, etc., to develop an integrated control program. Integrated control of a single pest species would be incorrect, excluding the given species of the ecosystem and ignoring the existing structure and interrelations present.

Nevertheless, and this is the main idea of our Multilateral control concept, the crop field as an ecosystem does not represent an isolated ecosystem, it has, as we have shown, many various more or less close connections with other ecosystems, which often are just an opposite as to their general character (forest-steppe). In such other ecosystems, we may find sources of the pest, etc. Therefore, we have to know the conditions existing in the other ecosystems with respect to the given pest species, before we could develop a certain integrated control program. Thus, we could briefly define the relationship between integrated control and multilateral control as follows: integrated control must be developed around a certain crop, the control of separate pest species must be multilateral.

REFERENCES. 67, 116, 125, 175, 228, 245, 247, 250, 295, 406, 408, 410, 414, 417, 421, 425, 479, 480, 487-8, 507, 630, 640-1, 679, 705, 714-8, 765, 871, 872, 942, 950, 1001, 1031, 1049, 1057, 1074, 1085, 1086, 1117, 1119, 1120, 1128, 1129, 1130, 1132, 1152, 1154, 1245, 1279, 1286, 1327.

Zusammenfassung

KAPITEL I: EINLEITUNG. Die Geschichte der Blattlausparasitenforschung entspricht im Entwicklungslauf den auf die parasitischen Gruppen der Hymenoptera allgemein gerichteten Untersuchungen. Der gegenwärtige Stand kann als Revision der bisherigen Erkenntnisse und als weitere, auf moderner Grundlage fortschreitende Entwicklung der Taxonomie charakterisiert werden, und ist gekennzeichnet durch das intensive Studium der Parasitenbiologie und den Einsatz von Parasiten bei der Bekämpfung der Blattläuse. Der Stand der Grundlagenforschung und angewandten Forschung ist gegenseitig befruchtend.

Die vorliegende Publikation stellt eine zusammenfassende Bearbeitung der Biologie der Blattlausparasiten dar. Eine solche Bearbeitung bietet insofern Vorteile, als sie eine zusammenhängende Einsichtnahme in verschiedene Aspekte vieler biologischer Fragen gewährt, die beim Studium von Teilfragen meist ausserhalb des Blickwinkels stehen. Das Buch enthält ferner zusammenfassende Anregungen für die Ausrichtung künftiger Arbeiten. Der Verfasser liess sich von der Idee leiten, für die Belange der Praxis eine komplexe Information über die gesamte Gruppe zu erarbeiten. Der schematische Aufbau entspringt der eigenen Konzeption des Verfassers; die relative Kompliziertheit der Arbeit ist durch das Bestreben gegeben, die verschiedenen Beziehungen klar ins Licht treten zu lassen. Jedes Kapitel enthält einen Schrifttumsnachweis, der den Weg zu ausgiebigerer Auskunft weist. Das Literaturverzeichnis wurde um die Mitte 1967 abgeschlossen.

KAPITEL II: METHODEN. In diesem Kapitel werden die fundamentalen Methoden der Materialsammlung, -einordnung, -aufbewahrung, -präparation und -bestimmung übersichtlich dargelegt. Die Aufmerksamkeit des Verfassers gilt auch der Aufzeichnung der gewonnenen Angaben und der Organisation der Sammlungen. Als geeignetste Methode der Materialgewinnung wird die Sammlung und Zucht von Blattlauskolonien in kleinen, durch Kunststoff verschlossenen Eprovetten angegeben. Über jede einzelne Zucht wird eine Aufzeichnung mit Angabe der Fundstätte, des Biotops, der Nahrungspflanze und der Blattlausart geführt. Bewährt hat sich die karteiformige Einordnung der Zuchten, desgleichen auch die Katalogisierung der Bestimmungsergebnisse mit Berücksichtigung der Parasiten- und der Wirtsart.

KAPITEL III: MORPHOLOGIE UND ANATOMIE. Die Eier der Blattlauswespen haben mikroskopische, form- und grossenspezifische Abmessungen. Es gibt 4 Larvenstadien, von denen das vierte die meisten spezifischen Merkmale aufweist. Es werden Morphologie und Anatomie der einzelnen Entwicklungsstadien des Parasiten, vom Ei bis zum Imago, untersucht.

KAPITEL IV: VERZEICHNIS DER GATTUNGEN UND UNTERGATTUNGEN DER GANZEN WELT. Der allgemeinen Übersicht über die Taxonomie der Gruppe dient die gemäss Konzeption des Verfassers aufgestellte Liste der Gattungen und Untergattungen der ganzen Welt.

KAPITEL V: BESTIMMUNGSSCHLÜSSEL DER GATTUNGEN UND UNTERGATTUNGEN DER GANZEN WELT. Der Bestimmungsschlüssel der Gattungen und Untergattungen der Welt ist reich illustriert, und ermöglicht die genaue Bestimmung jeder Blattlausparasitengattung.

KAPITEL VI: BIONOMIE UND ENTWICKLUNGSGESCHICHTE. In diesem sehr umfangreichen Kapitel werden untersucht: Evolution der Parasiten, ihr Verhalten, Lebensdauer und Nahrung der Imagines, Kopulation, zahlenmässiges Verhältnis der Geschlechter, Eiablage, Reproduktionskapazität, Entwicklungsdauer, Dispersion, saisonbedingter Lebensverlauf, Wirtsspezifität, Kategorien innerhalb der Arten, gegenseitiger Einfluss und Adaptation von Parasit und Wirt, Beziehungen zwischen verschiedenen Blattlausgruppen und ihren Parasiten, Ausdehnung auf einen nicht-natürlichen Wirt, Beziehungen innerhalb und zwischen den Arten. Beziehung von Parasiten und Ameisen. Die natürlichen Feinde der Parasiten.

Aus dem von Weibchen des Parasiten in die Blattlaus gelegten Ei schlüpft die Larve, die sich vorwiegend osmotisch ernährt: die erwachsene Larve frisst die Gewebe des Wirtes, tötet ihn und verpuppt sich innerhalb des Kokons. Der Kokon des Larvenparasiten kann sich entweder innerhalb oder ausserhalb der Wirtsblattlaus befinden. Die schlüpfende Imago besst sich aus der Puppe durch ein kreisförmiges Loch und schlüpft. Die Lage der Schlüpföffnung ist bei den einzelnen Gruppen verschieden. Als Nahrung dient den Imagines vor allem Honigtau der Blattläuse. Die Begattung hat weitgehenden Einfluss auf das Verhalten der Imagines, wobei das Prä- und Postkopulationsverhalten bei Männchen und Weibchen verschieden ist. Bei Parasiten gibt es im wesentlichen 3 Arten der Vermehrung: Arrhenotokie, Deuterotokie und Thelyotokie. Das zahlenmässige Geschlechtsverhältnis ist durch eine Reihe von Faktoren bedingt. Die Eiablage hat bei allen Blattlauswespen ähnlichen Charakter, sie weicht jedoch in spezifischen Details ab. Die Parasiten können sich aktiv oder passiv vermehren. Das Saisonvorkommen der Blattlauswespen ist durch eine ganze Reihe von Umweltfaktoren bedingt. Eine grosse Rolle kommt der Anpassung an den Lebenszyklus der Wirtsblattlaus zu. Die Parasiten sind im wesentlichen stenotop, zum Unterschied von den Blattläusen, wo eine Reihe von Arten die Fähigkeit besitzt, im Zusammenhang mit dem gesetzmässigen Wechsel der Wirtspflanzen auch die Biotope zu wechseln. Die Wirtsspezifität der Schmarotzer muss als ein Komplex der Erfordernisse aller Entwicklungsstadien erachtet werden, wobei die Hauptaufgabe den physikalischen und floristischen Faktoren, dem Biotop, der Gemeinschaft, dem Wirt und den artspezifischen Eigenschaften des Parasiten zukommt. In der Beziehung von Parasit und Wirt sind Beziehungen zwischen Arten (Populationen) und Beziehungen zwischen Individuen zu unterscheiden. In Bezug auf die Beziehung zwischen Parasiten und Wirtsgruppen sind letztere taxonomisch und morphologisch-ökologisch zu unterscheiden, da beiden Aspekten im Zusammenhang mit der Wirtsspezifität des Parasiten verschiedene Bedeutung zukommt. Die Ablenkung auf einen nichtnatürlichen Wirt verläuft im wesentlichen in zwei Richtungen: auf der einen Seite kommen solche Wirte in Betracht, die dem natürlichen Wirt des jeweiligen Parasiten verwandt sind, und zu Zwecken der Massenzucht angewandt werden; auf der anderen Seite ist es die Fortpflanzung von wirksamen Parasiten auf einen neuen Wirt – den Schädling. Innerhalb der artbedingten Beziehun-

gen kommt dem Superparasitismus als Faktor, der die Population des Parasiten im gegebenen Ökosystem regelt, grundlegende Bedeutung zu. Im Rahmen der Beziehungen zwischen den einzelnen Arten wird der Parasit als Mitglied eines Komplexes von natürlichen Blattlausfeinden betrachtet, unter denen es 3 Gruppen gegenseitiger Beziehungen gibt: Zusammenwirken, Konkurrenz und Verdrängung. In der Beziehung zwischen Parasiten und den die Blattläuse schützenden Ameisen liegt überwiegend indifferentes Verhältnis vor. Die natürlichen Feinde der Parasiten können entweder fakultativ oder obligatorisch vorhanden sein und schliessen eine ganze Reihe von Organismen, vor allem Insekten, ein.

KAPITEL VII: PHYLOGENESE. Zur Festlegung der hauptsächlichlichen Entwicklungsrichtungen wurden für Parasiten die Kriterien der geographischen Verbreitung, der Taxonomie, der Wirtsspezifität und der Fossilien angewandt. Die Blattlausparasiten kann man in ihrer Gesamtheit als eine progressive Gruppe betrachten. Es lassen sich einige natürliche Gruppen unterscheiden, die man jedoch wegen der Ungleichartigkeit der in Anwendung gebrachten Kriterien vorläufig besser ohne nomenklatorische Bezeichnung belässt.

KAPITEL VIII: VERBREITUNG IN DER WELT. Die Parasiten sind im wesentlichen an die einzelnen floristischen Zonen und ihre Evolution gebunden. Infolgedessen kann man heute eine Reihe von faunistischen Komplexen und von parasitären Hauptentwicklungszentren unterscheiden. Die unter den faunistischen Komplexen bestehenden Beziehungen sind sowohl für das Verständnis der Evolution der Fauna, wie auch für die Einfuhr der Parasiten im Rahmen der biologischen Schädlingsbekämpfung von Bedeutung. Das Studium der Inselfaunen hat gezeigt, dass die kontinentnahen Inseln eine ähnliche, jedoch ärmere Fauna als die benachbarten Kontinente besitzen, während die Fauna der ozeanischen Inseln sehr heterogen ist.

KAPITEL IX: NATÜRLICHE HERDE. Die Klassifizierung der in der Natur vorkommenden Parasiten ist eine der Grundvoraussetzungen für die Einschätzung ihrer Aufgabe als Regulatoren der Blattlausehäufigkeit, vor allem in einer Landschaft von landwirtschaftlichem Charakter. Von diesem Blickpunkt wurden Methoden der Erforschung von Herden, ihrer Typisierung und Einschätzung in Bezug auf die Stabilität des jeweiligen Ökosystems ausgearbeitet. Es wird eine ausgedehnte instruktive Übersicht der parasitären Herde in verschiedenen Gebieten der Welt, insbesondere in Mittel- und Südeuropa, und ferner im Kaukasus, in Mittelasien und Kuba gegeben, so dass im wesentlichen alle klimatischen Gebiete und die hauptsächlichlichen floristischen Zonen vertreten sind. Dies ebnet auch weiteren Bearbeitern den Weg. Besondere Aufmerksamkeit wird auch dem Problembereich der ariden Gebiete gewidmet.

KAPITEL X: NATÜRLICHE VORKOMMENSMÖGLICHKEIT DER BLATTLÄUSE. Eine kritische Auswertung und Vereinheitlichung der Sammlungsmethoden ist bei der Verfolgung der Populationsdynamik der Blattläuse und ihrer Parasiten Vorbedingung der Vergleichbarkeit der Ergebnisse. Um die Beziehungen zwischen Wirts- und Parasitenpopulationen eingehender untersuchen zu können, ist es erforderlich, über die Rolle des Parasiten im gegebenen Ökosystem, die dem Einfluss der Umweltfaktoren unterliegt, tiefere Einsicht zu gewinnen. Die Umweltfaktoren teilen wir ein in solche, die von der Populationsdichte abhängig, und solche, die von derselben unabhängig sind. Man kann den Wirkungsgrad der von der Populationsdichte abhängigen Faktoren als die Gesamtheit von Auswirkungen auffassen, die einerseits durch die Ergebnisse der Autoregulation innerhalb der Wirts- und Parasitenpopulationen, und

andererseits durch die Auswirkungen der Regulationskräfte des Ökosystems (Tätigkeit der natürlichen Feinde), gegeben ist. Eine Reihe dieser Faktoren kann sowohl unter Laboratoriumsbedingungen als auch im Freiland bestimmt werden. Der Wirkungsgrad des Parasiten ist als ein relativer Wert einzuschätzen, der durch eine Reihe von Faktoren beeinflusst wird.

KAPITEL XI: BIOLOGISCHE BEKÄMPFUNG DER BLATTLÄUSE. In den einführenden Teilen werden die allgemeinen Grundsätze der biologischen Schädlingsbekämpfung und die Auswertung der Blattläuse als Bekämpfungsgegenstand einer Betrachtung unterzogen. Es wird eine zusammenfassende Anleitung für die Einrichtung eines der biologischen Bekämpfung dienenden Laboratoriums gegeben. Das Programm der biologischen Bekämpfung beginnt mit der Klassifizierung des Ökosystems, der Pflanze, des Schädlings, und der örtlichen Parasiten. Es werden unter Berücksichtigung dieser Faktoren örtliche wie auch eingeführte Parasiten benutzt. Die Parasiteneinfuhr ist ein komplizierter Prozess, bei dem in der ersten Phase die Weltarten klassifiziert, und die für die Einführung geeigneten Arten ausgesondert und gesammelt werden. Dieses Material wird dann auf Grund spezieller Verfahren auf den Bestimmungsort gebracht. Daraufhin folgt die Laboratoriums- und Freilandsphase der biologischen Schädlingsbekämpfung. Es wird eine Übersicht aller für Blattlausparasiten in Anwendung kommenden Methoden gegeben. Hinzugefügt sind Übersichten der biologischen Schädlingsbekämpfung innerhalb der einzelnen Zonen, auf Inseln, in Glashäusern, in den einzelnen Ländern und Biotopen; ferner eine Übersicht der Blattlausarten als Objekt der biologischen Schädlingsbekämpfung und der Parasiten.

KAPITEL XII: INTEGRIERTE BLATTLAUSBEKÄMPFUNG. Die Einleitung des Kapitels ist einer gedrängten Betrachtung der Grundsätze der integrierten Schädlingsbekämpfung sowie der Auswertung der Blattläuse und ihrer Parasiten gewidmet.

Das Programm der integrierten Schädlingsbekämpfung beginnt mit der Auswertung des Ökosystems und des Schädlings. Die Grundlage bildet die natürliche Regulation des Schädlings durch Parasiten (Natürliche Feinde) und die biologische Bekämpfung im allgemeinen; ihre Auswirkung wird ergänzt durch kulturtechnische, chemische oder physikalische Massnahmen. Die einzelnen Methoden der Bekämpfung werden in übersichtlicher Form besprochen. Angeschlossen ist eine Übersicht der integrierten Schädlingsbekämpfung in den einzelnen Zonen, Ländern, Biotopen und Pflanzen, und ferner eine Übersicht der Blattlausarten als Objekte der integrierten Schädlingsbekämpfung sowie ihrer Parasiten.

KAPITEL XIII: MULTILATERALE BLATTLAUSBEKÄMPFUNG. Dieser Aspekt, eine Originalauffassung des Verfassers, unterstreicht die Vielseitigkeit der Voraussetzungen und Möglichkeiten zur Blattlausbekämpfung. Die integrierte Bekämpfung richtet sich auf ein bestimmtes Ökosystem (Pflanze), wobei jedoch besonders bei Blattläusen auch die Bedingungen anderer Ökosysteme, die als Schädlingsreservoir in Frage kommen, in Erwägung gezogen werden.

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ABBREVIATIONS: BC = BIOLOGICAL CONTROL, FC = FAUNISTIC COMPLEX,
IC = INTEGRATED CONTROL.
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Acanthodermes quercus KOLL.

Acyrthosiphon bidenticola SMITH

— *caraganae* CHOL.

— *gossypii* MORDV.

— *pisum* HARRIS

— *spartii* KOCH

— *superbini* BÖRN.

Allocotaphis gnarstioni BÖRN.

Amphorophora ampullata BECKT.

Anuraphis niddletoni THOMAS

— *subterranea* WALK.

Aphis abbreviata PATCH

— *acanthi* SCHRK.

— *agatheriae*

— *bambusae* MONR.

— *bupleuri* BÖRN.

— *cerasifoliae* FITCH

— *chioris* KALT.

— *chrysanthemi* WILS.

— *clematidis* KOCH

— *cognatella* JONES

— *corcopsidis* THOMAS

— *cornifoliae* FITCH

— *crataegae* L.

— *crataevora* KOCH

— *cusutae* DAVIS

— *cytisorum* Htg.

— *epilobii* KALT.

— *euphorbiae* KALT.

— *fabae* SCOP.

— *farinosa* GMEL.

— *frangulae* KOCH

— *gali-scabri* KALT.

— *genistae* SCOP.

— *gossypii* GLOV.

— *grossulariae* KALT.

— *hederae* KALT.

— *helianthi* MON.

— *heraclella* DAVIS

— *idaei* V.D.G.

— *illinoisensis* SHIMER

— *intybi* KOCH

— *klimeschi* BÖRN.

— *laburni* KALT.

— *laubersi* BÖRN.

— *lutescens* MON.

— *malvifoliae* FITCH

— *medicaginis* KOCH

— *mordwilckiana* DOBROWL.

— *nasturtii* KALT.

— *nerii* B.D.F.

— *neogillei* PALMER

— *neomexicana* COCK.

— *neoreticulata* THEO.

— *newtoni* THEO.

— *oenotherae* OESTL.

— *oestlundii* GILL.

— *origani* PASS.

— *phaceliae* G. and P.

— *plantaginis* SCHRK.

— *podagrariae* SCHRK.

— *polygonata* NEVS.

— *pomi* DEG.

— *poterii* BÖRN.

— *pseudohederae* THEO.

— *punicae* PASS.

— *ramouae* SWAIN

— *rharnii* FONS.

— *ruborum* BÖRN.

— *rumicis* L.

— *salviae* WALK.

— *sambuci* L.

— *sarothamni* FRANSS.

— *scaliai* D.G.

— *schneideri* BÖRN.

— *sedii* KALT.

— *solanella* THEO.

— *spiraeola* PATCH

— *spiraeophaga* HOLMAN

— *stachydis* MORDV.

— *saraxacicola* BÖRN.

— *thomasi* BÖRN.

— *umbrella* BÖRN.

— *urticata* KALT.

— *vallei* H.R.L. and STROYAN

— *vandergooti* BORNER

— *verbasci* SCHRK.

— *viburni* SCOP.

Aulacorthum aegopodii BÖRN.

— *chelidonii* KALT.

— *dryopteridis* HOLMAN

— *geranii* KALT.

— *solani* KALT.

Boernerina depressa BRAMST.

Brachycandus ballotae PASS.

— *calligoni* NEVS.

— *cardui* L.

— *helichrysi* KALT.

— *lychnidis* L.

— *mordwilckoi* H.R.L.

— *rumexicolens* PATCH

— *salsolaccarum* NEVS.

— *saxaulicae* NEVS.

— *tragopogonis* KALT.

Brachycolus noxius MORDV.

Brevicoryne brassicae L.

Buchneria pectinatae NORDL.

Byrsocrypta ulmi L.

Microlophium evansi THEO.
Astrosiphium millefolii WAHLGR.
 - *nudum* HOLMAN
Mitotarsus cyparissiae KOCH
Monellia caryae MON.
 - *costalis* FITCH
Myzaphis beibienkoi NARZ.
 - *rosarum* KALT.
Myzella galeopsidis KALT.
Myzocallis carpini KOCH
 - *coryli* GOETZE
Myzus ajugae SCHOUT.
 - *auctus* WALK.
 - *cerasi* F.
 - *houghtoniensis* TROOP.
 - *ligustri* MOSL.
 - *ornatus* LAING
 - *persicae* SULZ.
Nasonovia nigra H.R.L.
 - *pilosellae* BÖRN.
 - *ribisnigri* MOSL.
Nectarosiphium rubi KALT.
Neomyzus circumflexus BCKT.
Oregma laevigata ZEHNT.
Pachypappa vesicalis KOCH
Paczoskia major BÖRN.
Passerina tetrarhoda WALK.
Pemphigus lichteustei TULLGR.
 - *spirothecae* PASS.
Pentalonia nigronervosa COQ.
Periphyllus mamontovae NARZ.
 - *villosus* HTG.
Phalangomyzus oblongus MORDW.
Phorodon humuli SCHRK.
Phyllaphis fagi L.
Prociphilus fraxini HTG.
Protaphis carlinae BÖRN.
Protolachnus agilis KALT.
Pseudobrevicoryne crysimi HOLMAN
Pterochloroides persicae CHOL.
Pterocomma pilosum BCKT.
 - *salicis* L.
Rhodobium porosum SAND.
Rhopalomyzus alpigenae BÖRN.
 - *ascalonicus* DONC.

- *poae* WILL.
Rhopalosiphoninus latysiphon THEO.
Rhopalosiphum dianthi SCHRK.
 - *maidis* FITCH
 - *nymphacae* L.
 - *oxyacanthiae* SCHRK.
 - *padi* L.
 - *prunifoliae* FITCH
Roeperia mardiali BÖRN.
Schizaphis graminum ROND.
 - *longicaudata* H.R.L.
 - *scirpi* Kittel
Schizolachnus pineti F.
Schizocura ulmi L.
Semiaphis dauci F.
 - *dauci sesselii* BÖRN.
Siphia flava FORBES
 - *maidis* PASS.
Sitobium avenae F.
 - *equiseti* HOLMAN
 - *fragariae* WALK.
 - *granarum* KIRBY
 - *luteum* BCKT.
 - *salviae* BARTL.
Slavum lentiscoides MORDV.
Staegeriella necopmata BÖRN.
Stagona xylostei DEG.
Stomaphis quercus L.
Symydobius oblongus V. HEYD.
Tetraneura hirsuta BAKER
 - *ulmi* L.
Thelaxes dryophila SCHRK.
Therioaphis ononidis KALT.
 - *trifolii* MON.
Tinocallis caryae-foliae DAVIS
 - *platani* KALT.
Titanosiphon artemisiae KOCH
Todolachnus abieticola CHOL.
Toxoptera aurantii B.D.F.
 - *citricidus* KIRK.
Tuberculoides annulatus HTG.
Tuberolachnus salignus GMEL.
Viteus vitifolii BÖRN.
Xerophilaphis plotnikovi NEVS

List of scientific names—parasites.

- Acanthocandus* SMITH
 - *candacanthus* SMITH
 - *schlingeri* MUESEBECK
 - *tisseti* SMITH
Aclitus FORSTER
 - *obscuripes* FORSTER
Aphidius NEES
 - *absinthii* MARSHALL
 - *alius* MUESEBECK
 - *areolatus* ASHMEAD
 - *avenae* HALIDAY
 - *aventaphis* FITCH
 - *caraganae* STARÝ
 - *cingulatus* RUTHE
 - *confusus* ASHMEAD
 - *equiseticola* STARÝ
 - *ervi* HALIDAY
 - *floridacensis* SMITH
 - *funebis* MACKAUER
 - *gifuensis* ASHMEAD
 - *hieraciorum* STARÝ
 - *hortensis* MARSHALL
 - *impressus* MACKAUER
 - *lonicerae* MARSHALL
 - *matricariae* HALIDAY
 - + *maximus* THEDBALD
 - *megoura* STARÝ
 - *nirotarsi* STARÝ
 - *nigrescens* MACKAUER
 - *nigripes* ASHMEAD
 - *obscuripes* ASHMEAD
 - *ohioensis* SMITH
 - *pascuorum* MARSHALL
 - *phalangomyzi* STARÝ
 - *picipes* NEES
 - *pisivorus* SMITH/syn. of *pulcher* BAKER/
 - *polygonaphis* FITCH
 - *pulcher* BAKER
 - *ribis* HALIDAY
 - *rosae* HALIDAY
 - *rubi* STARÝ
 - *salignae* WATANABE
 - *salicis* HALIDAY
 - *setiger* MACKAUER
 - *sicarius* MACKAUER
 - *smithi* SHARMA and SUBBA RAO
 - *sonchi* MARSHALL
 - *tanacetarius* MACKAUER
 - *transcaspicus* TELENGA
Archaphidius STARÝ and SCHLINGER
 - *greenideae* STARÝ and SCHLINGER
 + *Archipraon* STARÝ in litt.
 - *gausai* QUILIS
Areopraon MACKAUER
 - *lepelleyi* WATERSTON
Bioxys STARÝ and SCHLINGER
 - *japonicus* STARÝ and SCHLINGER
Boreogalba MACKAUER
 - *gladifer* MACKAUER
Calaphidius MACKAUER
 - *elegans* MACKAUER
Chactopauesia MACKAUER
 - *talis* MACKAUER
Diactetellus STARÝ
 - *ephippium* HALIDAY
 - *hemzei* MACKAUER
 - *macrocarpus* MACKAUER
 - *pabustris* STARÝ in litt.
Diactetiella STARÝ
 - *rapae* M'INTOSH
Diaeretus FORSTER
 - *leucopterus* HALIDAY
Dyscritellus HENCKS
 - *planiceps* MARSHALL
Ephedrus HALIDAY
 - *brevis* STELFOX
 - *californicus* BAKER
 - *campestris* STARÝ
 - *cerasicola* STARÝ
 - subg. *Ephedrus* s. str.
 - *incompletus* PROVANCHER
 - *lacertosus* HALIDAY
 - subg. *Lysephedrus* STARÝ
 - *minor* STELFOX
 - + *mirabilis* TIMON-DAVID
 - *nacheri* QUILIS
 - *persicae* FROGGATT
 - *plagiator* NEES
 - + *primordialis* BRUES
 - *validus* HALIDAY
 + *Holomonius* QUILIS
 - + *braconiformis* QUILIS
Lipolexis FORSTER
 - *gracilis* FORSTER
 - *oregmae* GAHAN
 - *scutellaris* MACKAUER
Lysaphidius SMITH
 - *adelocarinus* SMITH
 - *arvensis* STARÝ
 - *erysimi* STARÝ
 - *placensis* BRETHES
 - *ramithytus* SMITH
 - *rosaphidius* SMITH
 - *schmitscheki* STARÝ
Lysiphlebia STARÝ and SCHLINGER
 - *japonica* ASHMEAD
 - *rigosa* STARÝ and SCHLINGER
Lysiphlebus FORSTER

- + *quievrenxi* QUILIS
- + *Propraon* BRUES
- + *cellularis* BRUES
- + *Protacanthoides* MACKAUER
- + *fuscus* QUILIS
- + *fossilis* MACKAUER
- Protaphidius* ASHMEAD
- *nawai* ASHMEAD
- *wissnani* RATZBURG
- + *Protephedrus* QUILIS
- + *terciarius* QUILIS
- + *Protodiactiella* STARÝ in litt.
- + *berdlandi* QUILIS
- + *Pseudaphidius* STARÝ in litt.
- + *cenozeicum* QUILIS
- + *fossiliferus* QUILIS
- + *lysiphleboides* QUILIS
- + *nigrofacies* QUILIS
- + *oligoanuidius* QUILIS
- + *oligocenus* QUILIS
- + *premedicoginus* QUILIS
- + *pseudogranarius* QUILIS
- + *saliniferus* QUILIS
- + *torneli* QUILIS
- Pseudephedrus* STARÝ
- *neotropicalis* STARÝ
- Tanytrichophorus* MACKAUER
- *petiolaris* MACKAUER
- Toxares* HALIDAY
- *deltiger* HALIDAY
- *shigai* TAKADA
- Trioxys* HALIDAY
- *acalephae* MARSHALL
- *amerceris* SMITH
- *angelicae* HALIDAY
- *asiaticus* TELENKA
- *auctus* HALIDAY
- *betulae* MARSHALL
- subg. *Betuloxys* MACKAUER

- subg. *Binodoxys* MACKAUER
- *bonnerilensis* SMITH
- *brevicornis* HALIDAY
- *brunneus* STARÝ and SCHLINGER
- *carinatus* STARÝ and SCHLINGER
- *centaureae* HALIDAY
- *cirsii* CURTIS
- *communis* GAHAN
- *complanatus* QUILIS
- *compressicornis* RUTHE
- *coruscantigrans* GAHAN
- *confucius* MACKAUER
- *salcatus* MACKAUER
- subg. *Fissicauda* s. STARÝ and SCHLINGER
- *genistae* MACKAUER
- *glaber* STARÝ
- *heraclei* HALIDAY
- *hortorum* STARÝ
- *humuli* MACKAUER
- *ibis* MACKAUER
- *indicus* SUBBA RAO and SHARMA
- *letifer* HALIDAY
- *luteolus* STARÝ and SCHLINGER
- *macroceratus* MACKAUER
- *orientalis* STARÝ and SCHLINGER
- *pallidus* HALIDAY
- *pannonicus* STARÝ
- *parauctus* STARÝ
- subg. *Pectoxys* MACKAUER
- *phyllophidis* MACKAUER
- *silvaticus* STARÝ
- *silvicola* STARÝ
- *sinensis* MACKAUER
- *spinosus* STARÝ
- *struma* GAHAN
- subg. *Trioxys* s. str.
- Xenostigmus* SMITH
- *bifasciatus* ASHMEAD